

THE AMERICAN NATURALIST

VOL. XLVI

November, 1912

No. 551

THE MENDELIAN NOTATION AS A DESCRIPTION OF PHYSIOLOGICAL FACTS

PROFESSOR E. M. EAST

BUSSEY INSTITUTION, HARVARD UNIVERSITY

As I understand Mendelism¹ it is a concept pure and simple. One crosses various animals or plants and records the results. With the duplication of experiments under comparatively constant environments these results recur with sufficient definiteness to justify the use of a notation in which theoretical genes located in the germ cells replace actual somatic characters found by experiment. This is done wholly to simplify the description of the experimental results. If one finds that the expression $DR \times DR = 1DD + 2DR + 1RR$ adequately represents the facts in numerous breeding experiments, he is then able to use the knowledge and the expression in predicting the results of other similar experiments. Mendelism is therefore just such a conceptual notation as is used in algebra or in chemistry. No one objects to expressing a circle as $x^2 + y^2 = r^2$. No one objects to

¹I do not speak here of the new biological facts discovered by Mendel or by his followers. Facts are always facts. Alternative inheritance and character recombinations were important facts, but I think no one will deny that the greatest value of Mendel's facts arose from the mathematical treatment he gave them. This mathematical notation remains conceptual just as does the chemical formula, but it must have as much basis of fact as there are pertinent facts extant.

saying that $\text{BaCl}_2 + \text{H}_2\text{SO}_4 = \text{BaSO}_4 + 2\text{HCl}$. No one should object to saying that $DR + RR = 1DR + 1RR$. We push things into the germ cells as we place the dollars in the magician's hat. Hocuspocus! They disappear! Presto! Out they come again! If we have marked our money we may find that that which appears from the magician's false-bottomed hat is not the same as that which we put in. But it looks the same and is good coin of the realm. We have a good right therefore to poke our characters into the germ cell and to pull them out again if by so doing we can develop—not a true conception of the mechanism of heredity—but a scheme that aids in describing an inheritance. We may do this even as we may use algebraical and chemical notations, if we remember that $x^2 + y^2$ does not give us a circle, that a chemical equation does not represent a true reaction or prove the atomic theory, that we have not pulled something new and astonishing out of the germ cell, that a unit factor represents an idea and not a reality, though it must have a broad basis of reality if it is to describe a series of genetic facts.

The facts of heredity that one describes in the higher organisms are the actual somatic characters, variable things indeed, but still things concrete. Their potentialities are transmitted to a new generation by the germ cells. We know nothing of this germ cell beyond a few superficial facts, but since a short description of the breeding facts demands a unit of description, the term unit factor has been coined. As I hope to show, a factor,² not being a biological reality but a descriptive term, must be fixed and unchangeable. If it were otherwise it would present no points of advantage in describing varying characters. The only obvious reason for poking it into the germ cell is to distinguish thus the actual parent (the cell) from the putative parent (the carrier).

² I hope this statement is not confusing. The term factor represents in a way a biological reality of whose nature we are ignorant just as a structural molecular formula represents fundamentally a reality, yet both as they are used mathematically are concepts.

If we forget ourselves and begin to speak of unit factors as particles, only a confusion follows similar to that caused by Nägeli, Spencer and Weismann. Nothing is gained and even facts are obscured.

THE SCOPE OF MENDELISM

How far may we carry this conceptual notation? My answer is: just as far as the notation interprets the facts of breeding and is helpful. Interest in the scope of Mendelism is now focused on two phases, complete and partial coupling and the interpretation of so-called size characters. Complete coupling in the transmission of characters apparently non-related has been shown in a large number of cases. Perhaps those best worked out in animals are the sex-coupled or sex-limited characters observed by Morgan in *Drosophila*. In plants, cases observed by Emerson and by Bateson and his coworkers are equally clear. Emerson has shown beyond a reasonable doubt that the characters he describes are independent of each other, and can not be represented by one factor. Bateson has recently corroborated the observation on other characters. Besides this phenomenon, Bateson has discovered partially coupled characters. All three of these writers, have subsidiary hypotheses to account for their facts. Bateson, when discussing perfect couplings, merely says that the characters come out in F_2 coupled in the way they went in in the grandparents, which naturally is only a restatement of the facts. Morgan and Emerson deal in pictures of carrying bodies. Both of their theories fit their own facts as they necessarily would. Emerson and, I may say, myself believe Morgan's theory incompatible with that of Emerson. Morgan believes his theory adequate for both cases. Without discussing the merits of these particular hypotheses I think it is agreed that some characters do go into the F_1 generation and come out from it together that are in other cases independent. The importance of the phenomenon is greater than the theory at present.

It has been questioned whether one has the right to continue to couple characters in large numbers to interpret facts, because by proper coupling one may interpret almost any fact, and place himself in a logically unassailable position. But this is no reason for not coupling factors as much as one pleases if it is helpful and if all of the facts fit. *A propos* of this statement I might say that I have recently remade the historical old cross first made by Kölreuter in 1760, *Nicotiana rustica* \times *Nicotiana paniculata*. These species differ in many details—habit of growth, size, shape and hairiness of leaf, inflorescence, and size and shape of flower and fruit. Both of the parent species have been reproduced exactly from a partially fertile F_1 in a total number of less than 200 F_2 plants. One may formulate an hypothesis of selective elimination of gametes combined with selective fertilization that helps to describe the facts, but unless large numbers of factors are coupled together I believe it to be impossible to account for all the facts by the usual Mendelian notation.

Before leaving this subject it might be mentioned that Bateson's theory, originated to account for partial coupling, keeps the idea of factors segregating from their absence, but instead of A and a being formed in equal quantities as in "regular" Mendelian notation, they are to be formed in series represented by the scheme $n-1AB:1AB:1aB:n-1ab$. I do not believe one should hasten to accept this description, although Bateson's F_2 generation facts certainly fit and have been recently supported by Baur. My reason for making this statement is that as yet Bateson's F_3 facts do not fit the theory. Some of them would even make necessary two or more different kinds of factorial distribution in the same plant varieties. On this score the helpfulness of our notation³

³ Here is a good illustration of the Mendelian notation as a concept. Supposing the gametic distribution $n-1AB:1Ab:1aB:n-1ab$ were to fit all the facts in the case, then no one could object to its use. If it were to be demonstrated that segregation occurred at the reduction division, however, the scheme no longer fits the facts and must be abandoned.

is impaired and this is the only excuse for its existence. Furthermore, while it has not been proved that the phenomenon we call segregation occurs at the reduction division, the presumption is in favor of that view. The work of Webber, Correns, Lock, Emerson and myself on *Xenia* in maize indicates that segregation does not take place immediately after reduction, while the work of the Marchals on regeneration in mosses indicates that it does not take place before reduction.

Now to turn to the kinds of variation that may be described by the Mendelian notation. Owing to its youth, we can all remember how we wondered, as each new case came up, whether Mendelian phraseology would fit. Since qualitative characters were the ones that could be divided into definite categories they were the ones attacked. One by one they were analyzed. The phraseology did fit. Qualitative characters however form a very small proportion of the characters in animals and plants. The numerous characters are the quantitative, the size characters. If Mendel's law is to be worth anything as a generality, therefore, it must describe the inheritance of these characters.

To some of us Mendel's law from the first seemed destined to be a notation generally useful in describing inheritance in sexual reproduction. This conclusion was indicated by the simple fact that Mendel's law described many cases in both the animal and the vegetable kingdom. It was inconceivable that this should be the result of coincidence. It was therefore still more inconceivable that only a small portion of the facts in each kingdom should come under the scope of Mendelism.

A basis for the inclusion of quantitative characters was obtained when Nilsson-Ehle and the writer showed that certain qualitative characters gave ratios of 15:1, 63:1, etc., in the F_2 generation, and in other ways behaved so that they might be described only by assuming more than one independent gametic factor as the germ cell representative of the character, if the orthodox idea of segregation were retained. From these phenomena

it was immediately seen that where dominance is absent and such multiple factors are assumed, size characters can be interpreted as coming under the Mendelian law. When dominance is complete the mathematical representation of an F_2 generation is $(3/4 + 1/4)^n$ where n represents the number of factorial differences involved; as the manifestation of dominance becomes less this formula approaches the type $(1/2 + 1/2)^{2n}$. The difference between the heredity of qualitative characters and quantitative characters is therefore only one of degree, for there is absence of dominance in cases of simple monohybrid qualitative characters and there is presence of multiple factors in cases of qualitative characters showing dominance. But it is manifestly absurd to expect size characters to appear in natural groups as do many qualitative characters. The marked effect of environment and our ignorance of the exact effect to attribute to each factor precludes it. One can determine whether size inheritance compares with the inheritance of qualitative characters only by the use of arbitrary biometrical methods. In theory, homozygotes with size differences when crossed should give an intermediate F_1 of low variability and an F_2 of high variability. Various F_3 populations should differ in their mean and in their variability. The difference in the variability of F_2 over F_1 should decrease as the heterozygosity of the parents increases. Sometimes parents of the same size should differ in the factors they contain and the F_2 generation should contain individuals smaller and individuals larger than either of the parents. Each of these requirements has been satisfied by experiment. East and East and Hayes have tested it for number of rows per cob, height of plant, length of ear and size of seed in maize, Shull for number of rows in maize, Emerson for fruit sizes in maize, beans and gourds, Tammes for various characters in flax species, Tschermak for time of blooming in beans, Hayes for number of leaves in tobacco, Belling for certain characters in beans, Phillips for body size in ducks, MacDowell for body size in rab-

bits. In these investigations every test possible for the theory has been satisfied. No criticism could be made except that certain of the characters used varied considerably in the mother varieties and therefore were presumably not homozygous for all character factors. This criticism is apparently answered by a recent investigation of the writer's, as yet unpublished, where two species, *Nicotiana forgetiana* and *Nicotiana alata grandiflora* were crossed. As seen by the table, the corolla length is very slightly variable in either species, nor is it affected to any extent by environment, yet each species was absolutely reproduced by recombination in the F_2 generation.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN
Nicotiana forgetiana (314) AND *N. alata grandiflora* (321).

| Designation | Class Centers in Millimeters | | | | | | | | | | | | | | | |
|------------------------------------|------------------------------|-----|----|----|-----|-----|-----|-----|-----|----|----|----|----|----|----|--|
| | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 | 85 | 90 | |
| 314 | 9 | 133 | 28 | | | | | | | | | | | | | |
| 321 | | | | | | | | | | 1 | 19 | 50 | 56 | 32 | 9 | |
| (314×321) _{F₁} | | | | 3 | 30 | 58 | 20 | | | | | | | | | |
| (314×321) _{F₂} | | 5 | 27 | 79 | 136 | 125 | 132 | 102 | 105 | 64 | 30 | 15 | 6 | 2 | | |

Coefficients of variation are: 314 = $8.86 \pm .33$ per cent.; 321 = $6.82 \pm .25$ per cent.; (314 × 321) F_1 = $8.28 \pm .38$ per cent.; (314 × 321) F_2 = 22.57 ± 39 per cent.

I do not believe that biologists have sufficient facts as yet to warrant any concrete meaning being given to their notation as regards germ-cell structure, but I do maintain that the Mendelian notation satisfies the facts of size inheritance as well as it satisfies the facts of qualitative inheritance. As a description, it goes the whole way. If qualitative inheritance is Mendelian, quantitative inheritance is Mendelian; if quantitative inheritance is not thus described, qualitative inheritance is described not a whit better.

All writers do not agree with this statement; nevertheless, speaking for myself only, I believe it to be beyond question. Castle (AMER. NAT., 46: p. 361) says:

It is quite possible that we are stretching Mendelism too far in

making it cover such cases. Dominance is clearly absent and the only fact suggesting segregation is the increased variability of the second as compared with the first hybrid generation. This fact however may be accounted for on other grounds than the existence of multiple units of unvarying power.

If size differences are due to quantitative variations in special materials within the cell, it is not necessary to suppose that these materials are localized in chunks of uniform and unvarying size, or that they occur in any particular number of chunks, yet the genotype hypothesis involves one or both of these assumptions. Both are unnecessary. Variability would result whether the growth-inducing substances were localized or not, provided only that they were not homogeneous in distribution throughout the cell. Crossing would increase variability beyond the first generation of offspring because it would increase the heterogeneity of the zygote in special substances (though not its total content of such substances) and this heterogeneity of structure would lead to greater quantitative variation in such materials among the gametes arising from the heterozygote. Thus greater variability would appear in the second hybrid generation.

I can not agree with this statement as I understand it, though this disagreement may be due to my own limitations. We do not stretch Mendelism and we do not make it cover such cases. The facts of breeding have been obtained and the Mendelian notation expresses them. That is all that it is necessary to claim. It is not precisely true, however, to say that increased variability in the second hybrid generation is the only fact to be expressed. It is of paramount importance that various F_2 individuals giving F_3 populations differing in mean and in variability, should be included in the Mendelian description. They are included.

Again, Castle states that the genotype conception assumes the localization of the hypothetical factors either in chunks of uniform and unvarying size, or that they are carried by a particular number of chunks. I am unaware of any such assumptions. It is true that some such picture has been suggested as a diagram helpful to the imagination in its conception of the scheme as a mechanical process, but this is purely and simply a diagram. The real matter under discussion is that the breeding facts are adequately described in a notation essentially Mendelian.

Of course Castle's scheme of expressing the facts by heterogeneity in the germ cell might serve. He produces increased variability in the second hybrid generation by greater differentiation among the gametes arising from the heterozygote. But one can also describe inheritance of qualitative characters in the same way, and one gains no system by it. It is a return to the type of expression used by Nägeli, Naudin and De Lage in pre-Mendelian days. It is simply a trans-nomination possessing no advantages.

Before leaving this phase of the subject, I must speak of Davis's recent fine paper (AMER. NAT., 46: p. 415) on his crosses between *Oenothera biennis* and *Oenothera grandiflora*. As I have had the advantage of seeing his cultures many times in the past two years, I am in a fair position to draw my own conclusions as to the meaning of his data. In regard to his F_2 generation from the hybrid plant marked 10.30 L b he says:

1. In the immensely greater diversity exhibited by the F_2 generation over that of the F_1 is clearly shown a differentiation of the germ plasm expressed by the appearance in the F_2 plants of definite tendencies in directions toward the two parents of the cross. This seems to the writer the essential principle of Mendelism and does not necessarily involve the acceptance of the doctrine of unit characters and their segregation in either modified or unmodified form.

2. Certain characters of the parent species have appeared in the F_2 segregates in apparently pure condition, but the very large range of intermediate conditions indicates that factors governing the form and measurements of organs (if present at all) must in some cases be concerned with characters so numerous and so small that they can not be separated from the possible range of fluctuating variations. If this is true such characters seem beyond the possibility of isolation and analysis and the unit character hypothesis for these cases has little more than a theoretical interest.

3. Both cultures certainly showed marked progressive advance in the range of flower size, the largest flowers having petals somewhat more than 1 cm. longer than those of the *grandiflora* parent. There was a similar advance in the size of the leaves and the extent of their crinkling. These progressive advances would seem to demand on the unit character hypothesis either the modification of the old or the creation of new factors.

4. The absence of classes among the F_2 hybrids (except for the

dwarfs) further works against the unit character hypothesis as of practical value in the analysis of a hybrid generation of this character. It should be remembered, however, that there were in this cross no sharply contrasted distinctions of color, anthocyan (stem) coloration proving most unsatisfactory for the purpose of a genetical study.

These four paragraphs are practically a résumé of Davis's genetic facts: I take exception only to some of the implied conclusions. It is quite evident that Dr. Davis believes that many breeding facts are expressed in shorthand by the Mendelian notation. His statements, however, imply a feeling of loss of caste or something of the kind if he makes definite use of Mendelian phraseology. His F_2 generation was exactly what would be expected when several Mendelian units without dominance segregate and recombine. The advance in size of corolla was predicted by me in 1910 (*AMER. NAT.*, 44: p. 81) as a direct consequence of size inheritance. It has since been demonstrated by Tschermak for time of blossoming of beans and clearly analyzed by Hayes for number of tobacco leaves. It demands neither modification of old nor the creation of new factors. It occurs whenever *AABB* (size factors) is crossed with *CCDD*, and each factor is allelomorphic to its own absence, to use the ordinary phraseology.

As to the difficulty of precise analysis into factors, I agree with Dr. Davis, but that there is no advantage in showing that this behavior is described in typical Mendelian terms I can not admit. One holds the same practical advantage here—though the case is complex—that one holds in all Mendelian inheritance. He knows that somatic appearance is not the criterion of breeding capacity, but that it is determined in some way by gametic constitution, although no germ cell architecture is presupposed. He knows that recombination of some kind of factors occurs and has some idea of the number of progeny to be grown to obtain the desired combination. In other words, the blend in F_1 does not indicate complete loss of extremes.

MENDEL'S LAW AND GALTON'S LAW

The above statement leads into a discussion of Mendel's law of heredity as compared with Galton's law, for in itself it is almost a statement of the difference. As Bateson was the first to emphasize, organisms inherit from parental germ cells only, therefore a law of ancestral heredity is a fallacy and a misnomer. The simple illustration that of two individuals alike in appearance one is homozygous for a character and the other heterozygous for the same character, shows the superficial reasoning that leads to the correlation coefficient as a measure of heredity. Parental and filial populations may show correlation, but that is only a matter of averages and not a measure of the inheritance.

Professor Castle has recently disclosed the probable Mendelian basis for Galton's data on coat color of Bassett hounds by showing the inheritance of tricolor coat in guinea-pigs, yet he makes the surprising statement that "as regards height, however, and other size characters, Galton's law is quite as good a basis for predicting the result of particular matings as is Mendel's." The arch priest of biometry, Karl Pearson, does not claim that Galton's law can predict the result of individual matings. Similarly, Mendel's law predicts only by averages. It says that where DR meets DR , there will be on the average $1DD:2DR:1RR$ produced. Where the classes are larger the prediction is increasingly complicated. But the prediction is as good for size characters as for qualitative characters of the same complication. And there are such qualitative complications, as is manifest by Castle's formula of $AACCUUIIYYBBBrBrEE$ for a wild rabbit's coat color. The difference between Galton's law and Mendel's law is that the true criterion of the germ plasm of any individual is its breeding power and not the somatic appearance of its back ancestry. This is as true of size characters as of any other characters.

THE GENOTYPE CONCEPTION OF HEREDITY

Expressed in Johannsen's words, the basis of the modern conception of heredity is: "Personal qualities are the *reactions of the gametes joining to form a zygote*; but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question." The quotation expresses well the idea that I have just tried to convey, and from it one sees plainly that it is the correlation that necessarily appears to a greater or less extent between the somatic qualities of two generations when they exist in large numbers that gave the basis for Galton's superficial law.

This quotation is Johannsen's slogan for the genotype conception of heredity. As there stated, it is merely a generalized expression of the essential features of the Mendelian notation. Johannsen, therefore, was the first to admit the broadness of its scope. In his exposition of his position, however, he adds two subsidiary propositions that we will now discuss; the first is the perennial question of the possibility of the inheritance of acquired characters, the second is a question which from its illusiveness is likely to take on a perennial habit—that of the relative constancy of unit characters.

In regard to the first question I must be content here with a mere general statement. Like Osborn I would emphasize the possibly delusively static condition of organisms when tested during the infinitesimal time usually devoted to experiment. The inheritance of acquirements in some subtle way unknown to us may have been of immense importance in evolution. On the other hand, some sort of an orthogenesis may account for all the facts without the inheritance of acquired characters. It scarcely seems possible that everything is mere chance, though one who has studied plant teratology is astounded at the almost infinite number of characters that have appeared that were absolutely dangerous to the individual in its contest for survival. Be that as it may, I simply wish to acknowledge unbelief in any so-called

proof that the inheritance of acquired characters is *impossible*. At the same time one must admit that no unquestionable proof of such inheritance has ever been submitted. Experimental evidence is woefully negative. It seems only reasonable, therefore, considering the available corroborative evidence, to relegate the expression of new characters to variations that have affected the potentialities of the germ cells. We can simply divide variations into the classes inherited and non-inherited without any admission as to their cause. We can call the inherited variations mutations if we will, or we can give them any other name. We must simply remember that they are both large and small.

One can hardly agree with Osborn that *large* variations which are not in an orthogenetic line have had little value in evolution, or that teratological phenomena are of little consequence. The production of identical quadruplets in the armadillo can scarcely be a gradually perfected character. Zygomorphism in flowers is lost as a unit and although this does not prove its birth as a unit, still that is to be presumed. One could fill pages with such data, but this is hardly the place for it. We will therefore consider the relative constancy of what we know as a unit character.

THE CONSTANCY OF UNIT FACTORS

The first thing one does if he wishes to oppose the idea of a unit character is to ask for a definition. A perfect definition of a unit character is as difficult to formulate as for a flower, yet one can obtain an idea of a flower by proper application. If one describes a unit character as the somatic expression of a single gametic factor or heredity unit, he at once gets into trouble. As the factor and not the character is the descriptive unit, a unit factor may affect a character but that character may never be expressed except when several units cooperate in ontogeny. I should prefer to disregard the word character therefore in formulating the problem. The real problem is: Are the facts of heredity ade-

quately described by unvarying hypothetical factors? It is my thesis that if they can not be so described, the Mendelian notation fails.

Johannsen was the first to show the relative constancy of characters by his beautiful experiments on beans. Since that time, experiments designed to show change, if present, have yielded negative results on bisexual animals such as poultry (Pearl), on plants such as peas (Love), beans (Johannsen's later work), maize (Shull, East, Emerson), on asexual animals such as hydra (Hanel), paramæcium (Jennings) and on asexual plants such as bacteria (Barber and others), and potatoes (East).

Three critics have appeared. Karl Pearson took up the gage of battle because Johannsen's work shows the utter untenability of the correlation coefficient as a measure of heredity. He has produced no evidence to uphold his view. Harris, following Pearson for a like reason, has concluded against Johannsen, but has not yet presented his data for public criticism. There remains the work of Castle, which he believes is supported by the work of Woltereck. The question to consider then is whether the work of these two investigators justifies the contention.

Castle states that by selection he has modified a unit character. No one questions that under certain conditions changes in characters are made manifest by selection. It has been done again and again. The question as I see it is the following: Are not the facts presented by Castle and the facts of the pure-line workers described most concisely and in a way most helpful to investigation, by the reactions of fixed and unchanging units? If they can not be thus described the use of units is an absurdity, for one can not measure or describe by changing standards.

Castle's principal work on selection is with a fluctuating black and white coat pattern—the so-called hooded rat. In writing of these experiments, Castle says (*l. c.*, p. 355):

I shall speak first of the case least open to objection from the genotype point of view, which requires:

1. That no cross breeding shall attend or shortly precede the selection experiment, lest modifying units may unconsciously have been introduced, and

2. That only a single unit-character shall be involved in the experiment.

These requirements are met by a variety of hooded rat which shows a particular black and white coat pattern. This pattern has been found to behave as a simple Mendelian unit-character alternative to the self-condition of all black or of wild gray rats, by the independent investigations of Doncaster, MacCurdy and myself. The pigmentation however in the most carefully selected race fluctuates in extent precisely as it does in Holstein or in Dutch Belted cattle. Selection has now been made by Dr. John C. Phillips and myself through 12 successive generations without a single out-cross. In one series selection has been made for an increase in the extent of the pigmented areas; in the other series the attempt has been made to decrease the pigmented areas. The result is that the average pigmentation in one series has steadily increased, in the other it has steadily decreased. The details of the experiment can not be here presented, but it may be pointed out (1) that with each selection the amount of regression has grown less, *i. e.*, the effects of selection have become more permanent; (2) that advance in the upper limit of variation has been attended by a like recession of the lower limit; the total range of variation has therefore not been materially affected, but a progressive change has been made in the mode about which variation takes place.

3. The plus and minus series have from time to time been crossed with the same wild race. Each behaves as a simple recessive unit giving a 3:1 ratio among the grandchildren. But the extracted plus and the extracted minus individuals are different; the former are the more extensively pigmented.

4. The series of animals studied is large enough to have significance. It includes more than 10,000 individuals.

The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit.

This conclusion, from the writer's standpoint, is not only avoidable, but unnecessary. No direct or implied denial of these facts is made, but a shift is made in the point of view. It seems to me a logical necessity that hypothetical units used as measurement or descriptive standards be fixed. The problem to be solved is the simplest means of thus expressing the facts. If the most

definite characters—i. e., certain pure-line homozygotes—are sufficiently constant in successive generations to be expressed by a fixed standard, well and good. The whole heredity shorthand is then simple. If such is not the case, the *character* must still be described by some fixed standard, but in that case recourse must be had to complex mathematical expressions and not to a single unit to describe the most constant somatic expressions. Furthermore, if these mathematical expressions served any practical purpose, it would be necessary to prove that all somatic variability of homozygotes under uniform conditions (if there is any) may be expressed by very few formulas.

Such an attitude does not seem to be in harmony with the progressive spirit of the times. I believe that we may describe our results simply and accurately by holding that unit factors produce identical ontogenetic expressions under identical or similar conditions. If under identical conditions the expression *is* different, then a new standard, a new unit, must be assumed; that is, factor *A* by any change becomes factor *B*. The results of the pure-line investigations are the warrant for this interpretation, for they are the investigations of successive generations of somatic expressions with the least attendant complication. From them one may assume that a succession of individuals homozygous in all characters and kept under identical conditions will be alike.⁴ To be sure there are numerous changes in the expression of characters when external and internal conditions are not so uniform as the above, but I believe that these changes can all be described adequately and simply by ascribing them to modifying conditions both external and internal. When external we recognize their usual effect in what we called non-inherited fluctuations, when internal we recognize their cause in other gametic factors inherited independently of the primary factor but

⁴ Possibly even under these conditions rare variations that are exceptions to this rule might occur. In other words, mutations might occur having no external cause and therefore to be left for vitalistic interpretation, but this would not affect the general situation.

modifying its reaction during development. This is a physiological conception of heredity, as it recognizes the great coöperation between factors during development. It is a very simple conception of heredity, moreover, for it allows a multitude of individual transmissible differences with the assumption of a very few factors. Some illustrations will be given later that will show the idea underlying this theory. Let us now see whether Castle's work can be described properly by it.

Castle started with a peculiar character. It fluctuates continually and has never been bred to as small a variability as have many other characters. I have worked with a somewhat similar character in maize. It is a variegated pericarp color. In experimenting with it I have raised over a thousand progeny in one generation, a thing manifestly impossible with rats. Both solid colored ears and white ears have been obtained, and while at present it would be unwise to draw definite conclusions, it appears that both solid red ears and white ears of this kind give again variegated progeny. In other words, neither the red ear nor the white can behave like a normal red or white ear, but as if the pattern had fluctuated so widely that it can not appear on the ear (this explanation was suggested by Emerson). At any rate, we may conclude that the rat pattern fluctuates widely and is therefore markedly affected by some condition either internal or external.

Castle began therefore with a character in a fluctuating condition, possessed by a race which had not recently been crossed with a different race. This does not mean, however, that the various individuals forming his original stock did not differ in several factors that in their different combinations might have an effect upon the developing pattern. Suppose for the moment that this were actually the case. If he had been able to produce a fraternity by a single mating numbering several thousands, he would have produced individuals with all of these combinations of other genes. It is probable that he would then have obtained his progressive ex-

extremes in one generation, extremes that were never seen when but few individuals were produced. This sort of a thing is not hypothetical. It is mathematically demonstrable that with the same variability $(a + b)^n$ expanded gives an increase in the number of classes as the total number of individuals increases. It is, moreover, supported by the experimental evidence of De Vries on selecting for higher number of rows in maize. I, myself, by using greater numbers obtained an increase in protein in maize in one generation comparable to that obtained by the Illinois Agricultural Station in three generations.

Castle further argues that decrease in regression toward the original mean supports his view. On the other hand, this is exactly what should take place on assuming the truth of the fixed factor conception, as has been shown by Jennings.

Again, the selected races when crossed with wild races both act as simple recessives, but the extracted plus individuals are more pigmented. This is what I should expect. The extracted plus individuals would be more pigmented when existing in small numbers, because the modifying factors are several. If several thousand progeny were grown, however, recombinations would show a more varied result. And as a matter of fact, extracted recessives from the plus race are not precisely comparable in their fluctuation to the selected race with which the wild was crossed. They are more variable than the progeny of an inbred hooded individual of the same grade as the parent used in the cross with the wild. I do not think that one has a right to say, therefore, that there were no modifying genes present in various combinations in the extracted recessives.

When the selected lines were crossed together, moreover, the resulting progeny were somewhat intermediate and variable. The grandchildren were *more* variable. This is what should result from our assumptions. The animals are homozygous as far as having a pattern is concerned, but they differ in several genes that affect the development of the pattern.

Taking into consideration all the facts, no one can deny that they are well described by terminology which requires hypothetical descriptive segregating units as represented by the term factors. What then is the object of having the units vary at will? There is then no value to the unit, the unit itself being only an assumption. It is the expressed character that is seen to vary; and if one can describe these facts by the use of hypothetical units theoretically fixed but influenced by environment and by other units, simplicity of description is gained. If, however, one creates a hypothetical unit by which to describe phenomena and this unit varies, he really has no basis for description.

The facts obtained when working with pied types are complex. They are evidently not thoroughly understood as is evidenced by a different interpretation made by every worker who has investigated them. Doncaster and Mudge see two types of Irish rat. Why not three or four? Crampe obtained hooded rats from cross of self-colored and albino, the hooded coming only from heterozygotes having some white. No adequate explanation has been given. Cuénot concluded regarding pied mice with several degrees of piedness that each was recessive to the other of next higher grade. In fact the behavior of self colors and spotted colors among mammals as among plants is pretty well "confused," as in several species spotted types dominant to self color are known.

Castle's other experiments in selection—the formation of a four-toed race of guinea-pigs starting with one animal with a rudimentary fourth toe, and the perfection of a silvered race of guinea-pigs from an animal in which the character was feebly expressed—need not be considered here. Both were necessarily crossed with normals at the start, and gradual isolation of races having the proper gene complex for complete expression of the characters is to be expected. There have been numerous selection experiments of this type—such as those of De Vries, the Vilmorins, the Illinois Agricultural Experiment Station, etc.—that have yielded results.

But these results, with one possible exception, were open to the criticism that they probably had to do with mixed lines and could therefore be described by the notation we have used. The experiments on pure lines have given no such results. One should not be asked to accept the results of the unguarded experiments and disregard the results of the guarded investigations.

The one possible exception alluded to above refers to the experiments of Woltereck (*Deut. Zool. Gesell.*, 19: 110-173, 1909) on parthenogenetic strains of *Hyalodaphnia* and *Daphnia* where there can be no question of gametic recombination. This experiment is not beyond criticism as will be seen later, but if it were our position would not be affected. The results would still have to be described by some *fixed standard* but the description would be complicated. *Since it is not beyond criticism, there is yet no reason for such a complication.*

Woltereck's work was primarily to show whether or not acquired characters are inherited. It was a secondary object to find out whether small variations or distinct sports occurred in the species. Those who use the work as an argument for unit factor modification, therefore, should also accept his inheritance of characters acquired.

Woltereck tested the effect of selection on seven characters. Selection gave *no* results in five cases. The first supposedly successful case is for difference in head height. In different pure lines he found an enormous effect of environment. He therefore endeavored to plot curves for different kinds of environment, food, temperature, generation number, etc. By comparing these curves he makes an argument for the inheritance of small acquired variations. In the absence of control cultures, and from the fact that culture conditions very uniform to Dr. Woltereck may have been somewhat extreme to Mr. A. Daphnia, the argument has only the value of the other numerous scholastic defences of inherited acquirements. It is criticized by Tower in a recent publication. Woltereck did obtain one inherited

head variation. It apparently arose suddenly. He calls it a mutation.

The only result that can be considered seriously from the standpoint taken in this paper is the result when selecting for a rudimentary eye. *Daphnia* has been distinguished from *Hyalodaphnia* by the presence of a rudimentary eye. The distinction does not seem to be valid, for Woltereck noticed rudimentary eyes several times in pure line cultures of *Hyalodaphnia* and they have also been seen by others in wild cultures. He regards the phenomenon as a reversion to a preexisting condition. *He found that the presence of the rudimentary eye is periodic. In the spring it appears, in the summer it again disappears.* Either kind can produce progeny of the other kind. From this fact it seems reasonable to believe that environment or generation number has much to do with the expression of the character, although Woltereck in one place inclines to the opinion that external factors affect it but little. He performed several experiments on the effect of light and temperature, however, and says that provisionally they gave no result free from objection—" . . . gegeben einstweilen kein einwandfreies Resultat." Almost any interpretation can be given this statement.

From a pure line in which this variable eye spot appeared, he isolated a mother and grandmother with the character well developed. Ninety per cent. of the progeny had the eye well developed. The rapidity of his results and the fact of *periodicity* in the expression of the character makes any cumulative effect of selection exceedingly questionable. One is not justified therefore in accepting it as proof without corroboration.

CONCLUSION

In conclusion, it may be asked if it is not reasonable to accept simply as a nomenclature the description of the whole facts of inheritance in sexual reproduction given by the Mendelian system? Is it wise to turn backward and to give up this handy and helpful notation

right in the midst of a useful career? The experiments least open to objection (the pure-line experiments) have shown the wisdom of assuming a stable unit factor, this factor being representative of the stability manifested by a character complex when no interfering conditions intervene. Let us accept this simple interpretation provisionally, appreciating the fact that the stability of the characters that have been represented by fixed units may be only a static appearance due to limited experiments; but that this appearance justifies our neglecting any infinitesimal fluency of our factor standards in experiments of like duration, since taking them into account would necessitate a change of standard, a new fabric of hypotheses and a more complicated system. Let us take a physiological view of heredity. Factors are assumed to be stable. Characters are somewhat unstable owing to the effect that other factors have upon their expression. Factor *A*, for example, is potentially able to produce a typical expression in ontogeny under certain definite conditions of environment, but the presence or absence of *B* or *C* or *D* or *B*, *C*, and *D* are responsible for slight changes in the expression of *A*. This conception gives us a picture of heredity in real accordance with physiological facts, in contradistinction to the non-biological and fixed physical conception—the mosaic organism conception—that critics often say is held by some geneticists.

One may answer that this conception is all right for quantitative characters, but do the facts uphold it for qualitative characters? They do. I will give examples from my own experiments on the inheritance of the purple aleurone cells in maize. Here one obtains progeny by the thousands and sees phenomena that are obscured by lesser numbers.

Crosses of the purple variety with three different whites have given three different results. One shows that the purple may be represented by the schematic description *PPRRCC*. Crossed with *pp rr cc* it gives purples, reds and whites in the F_2 generation, as all three

factors are necessary for the production of the purple color. How many other factors (present also in the whites) may be necessary one can not say. In another white, the *R* factor is present and purples and whites in the ratio of 9:7 result. In another white, both *P* and *R* are present. In another white, both *P* and *C* are present. Both give monohybrid ratios when crossed with the purple.

This is not the sum total of whites, however; several others have been found. One has an intensifying factor. We get darker purples together with the normal purples, but no one can doubt that the purple is still the same pigment modified in its expression. Another white has a dominant inhibiting factor. In the heterozygous condition it does not always inhibit the color entirely, but in the homozygous condition color never develops. The dominance of this factor is proved by the fact that extracted colored recessives are still heterozygous for presence of color.

In still other whites I have demonstrated the presence of at least three modifying genes $M_1M_2M_3$. They are independent of each other, yet each and all affect the purple color. One is dominant, as if it were a partial inhibitor, the others are recessive, as if they were the loss of intensifying factors. Purples of all different degrees can be isolated and breed true. The lightest is such that the color can be distinguished only with a lens. But they are all strictly alternative in their transmission and somewhere near the expected ratios of darks, lights, very lights, etc., appear. It is too much to ask that exact ratios be obtained for with this kind of modification all shades appear, yet conclusive evidence has been obtained by F_3 and F_4 generations.

The qualitative characters do act the same as quantitative characters, therefore, and one can not make a real distinction between them.

A FIRST STUDY OF THE INFLUENCE OF THE
STARVATION OF THE ASCENDANTS UPON
THE CHARACTERISTICS OF THE DE-
SCENDANTS—II¹

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

III. PRESENTATION OF DATA AND COMPARISON OF CON-
STANTS FOR NAVY, WHITE FLAGEOLET AND NE PLUS
ULTRA BEANS.—*Continued*

B. Number of Ovules per Pod.

The nature of this and the following character has been discussed elsewhere.² There the data from which all the physical constants necessary in this study may be deduced, but not the constants themselves, are set forth. Tables IX–XI give these constants based on countings of ovules formed and seeds matured in 130,074 pods.

That the starvation of the individual affects not merely the number of pods which it produces but the characteristics of these pods as well is evident from a study of these tables, but is best brought out by a special kind of graph.

Reducing absolute to relative frequencies, we take the difference

Starved *less* fed

for each ovule grade. Such differences are shown in Diagram 8 for *NDD–NDH*, *NDDC–NDHC*, *NHD–NHH*, *NHDC–NHHC*, *USD–USH*, *USDC–USHC*, *FSD–FSH* and *FSDC–FSHC*. The differences for the ancestral series, which for the moment alone interest us, are shown

¹ The first part of this paper appeared in this journal, Vol. 46, pp. 313–343, 1912. The reader must consult it for all questions of purpose, materials, methods, etc.

² Harris, J. Arthur, "On the Relationship between Bilateral Asymmetry and Fertility and Fecundity," *Roux's Archiv.* In press.

by the positions of the circles while those for their off-spring grown upon the comparison field are represented

TABLE IX

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>NH</i> | 5.7170 \pm .0106 | .7762 \pm .0075 | 13.5763 \pm .1335 |
| <i>NHH</i> | 5.4126 \pm .0049 | .8569 \pm .0035 | 15.8323 \pm .0653 |
| <i>NHHH</i> | 5.3706 \pm .0049 | .7669 \pm .0035 | 14.2803 \pm .0656 |
| <i>NHD</i> | 4.7192 \pm .0080 | .8890 \pm .0057 | 18.8383 \pm .1245 |
| <i>NHDD</i> | 4.9985 \pm .0074 | .8064 \pm .0052 | 16.1313 \pm .1069 |
| <i>ND</i> | 4.0034 \pm .0120 | .6829 \pm .0085 | 17.0587 \pm .2181 |
| <i>DDD</i> | 4.3503 \pm .0138 | .7695 \pm .0098 | 20.1638 \pm .2340 |
| <i>DDDD</i> | 4.7161 \pm .0163 | .7083 \pm .0080 | 15.0181 \pm .1630 |
| <i>NDH</i> | 5.1375 \pm .0070 | .7957 \pm .0049 | 15.4881 \pm .0980 |
| <i>NDHH</i> | 5.1692 \pm .0067 | .7057 \pm .0048 | 13.6517 \pm .0936 |
| <i>NHHC</i> | 5.6607 \pm .0109 | .7852 \pm .0077 | 13.8708 \pm .1389 |
| <i>NHHHC</i> | 5.5853 \pm .0107 | .8099 \pm .0076 | 14.4999 \pm .1381 |
| <i>NHDC</i> | 5.6295 \pm .0137 | .8466 \pm .0097 | 15.0390 \pm .1762 |
| <i>NHDDC</i> | 5.6573 \pm .0104 | .7371 \pm .0073 | 13.0289 \pm .1315 |
| <i>NDCC</i> | 5.3701 \pm .0147 | .7409 \pm .0104 | 13.7965 \pm .1969 |
| <i>DDDDC</i> | 5.5337 \pm .0127 | .7397 \pm .0090 | 13.3674 \pm .1652 |
| <i>NDHC</i> | 5.4800 \pm .0104 | .7016 \pm .0073 | 12.8031 \pm .1362 |
| <i>NDHHC</i> | 5.4046 \pm .0096 | .7133 \pm .0068 | 13.1973 \pm .1282 |

TABLE X

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>USS</i> | 5.5279 \pm .0072 | .8694 \pm .0051 | 15.7280 \pm .0945 |
| <i>USH</i> | 5.1491 \pm .0095 | .8196 \pm .0067 | 15.9178 \pm .1333 |
| <i>USHH</i> | 5.2392 \pm .0116 | .7151 \pm .0082 | 13.6483 \pm .1588 |
| <i>USD</i> | 4.7706 \pm .0207 | .8705 \pm .0147 | 18.2481 \pm .3174 |
| <i>USDD</i> | 4.7991 \pm .0174 | .7531 \pm .0123 | 15.6925 \pm .2628 |
| <i>USC</i> | 5.5866 \pm .0093 | .6978 \pm .0066 | 12.4908 \pm .1194 |
| <i>USSC</i> | 5.6992 \pm .0109 | .6992 \pm .0077 | 12.2692 \pm .1367 |
| <i>USHC</i> | 5.5548 \pm .0125 | .7348 \pm .0088 | 13.2290 \pm .1620 |
| <i>USHHC</i> | 5.5713 \pm .0117 | .7622 \pm .0083 | 13.6816 \pm .1511 |
| <i>USDC</i> | 5.5287 \pm .0117 | .7377 \pm .0083 | 13.3431 \pm .1522 |
| <i>USDDC</i> | 5.5244 \pm .0121 | .7236 \pm .0086 | 13.0989 \pm .1579 |

TABLE XI

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>FSS</i> | 5.6864 \pm .0080 | 1.0530 \pm .0057 | 18.5181 \pm .1033 |
| <i>FSH</i> | 5.5580 \pm .0077 | .7639 \pm .0054 | 13.7443 \pm .0991 |
| <i>FSHH</i> | 5.5150 \pm .0075 | .6873 \pm .0053 | 12.4619 \pm .0974 |
| <i>FSD</i> | 4.9579 \pm .0142 | .8022 \pm .0101 | 16.1798 \pm .2080 |
| <i>FSDD</i> | 5.0193 \pm .0116 | .6799 \pm .0082 | 13.5471 \pm .1668 |
| <i>FSC</i> | 6.0960 \pm .0097 | .7728 \pm .0069 | 12.6768 \pm .1145 |
| <i>FSSC</i> | 6.1840 \pm .0106 | .7816 \pm .0075 | 12.6390 \pm .1235 |
| <i>FSHC</i> | 6.0761 \pm .0121 | .8273 \pm .0086 | 13.6149 \pm .1437 |
| <i>FSHHC</i> | 6.0245 \pm .0098 | .8173 \pm .0069 | 13.5660 \pm .1168 |
| <i>FSDC</i> | 6.0525 \pm .0137 | .7853 \pm .0097 | 12.9756 \pm .1621 |
| <i>FSDDC</i> | 6.0616 \pm .0107 | .8144 \pm .0076 | 13.4355 \pm .1268 |

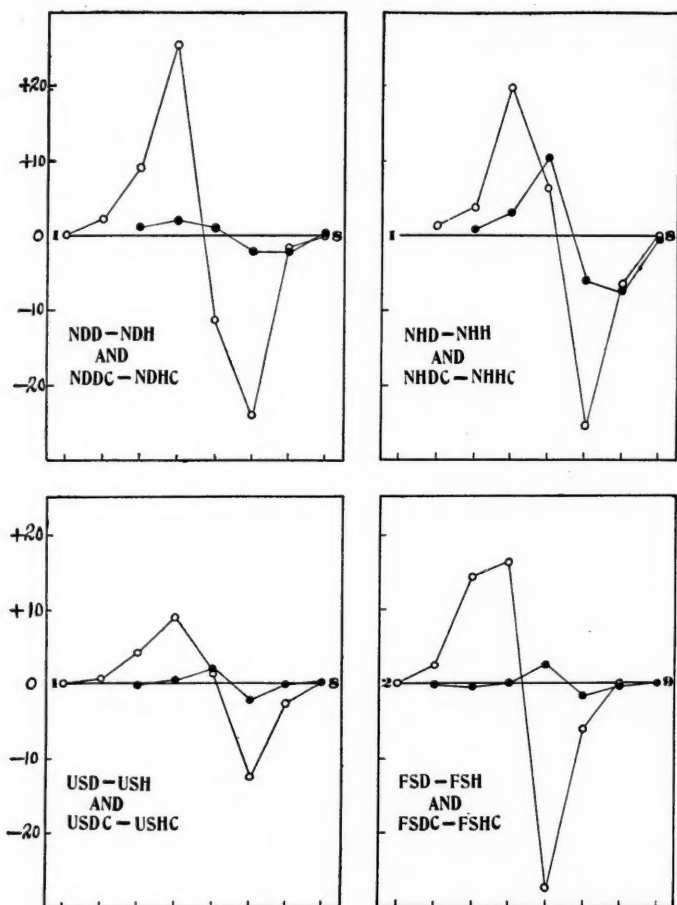


DIAGRAM 8. Differences in the percentage frequencies of various numbers of ovules per pod in luxuriant and depauperate cultures and in their offspring.

by solid dots. A profound influence of the starvation conditions is evident from these graphs. Relatively, the lower grades are much in excess, the higher grades much in defect in the starvation series.

The same fact is quite patent when one deals with the means of the series instead of comparing individual classes in the same lot. Clearly from Diagram 9:

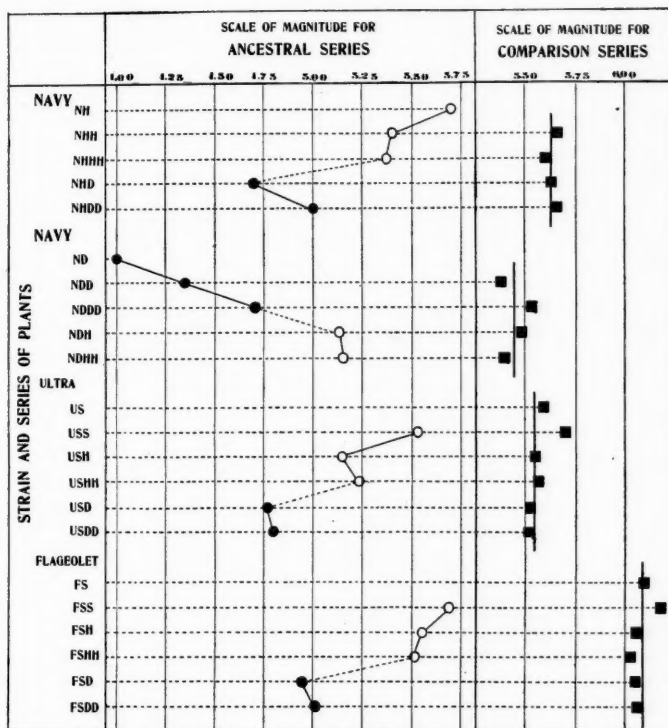


DIAGRAM 9. Mean number of ovules per pod. Compare explanation of diagram 6.

(a) The means are in every case conspicuously lower for the starved than for the fed ancestral series.

(b) The means for the comparison series are closely similar: there is no striking superiority of fed over starved ancestry.

Here, accordingly, as for number of pods per plant, we must have recourse to numerical differences and their probable errors. The intra-ramal comparisons are made in Table XII. In three of the four cases, the starved seeds produce pods with more ovules, but in all cases the seed was a year older for one generation of ascendant

TABLE XII

| Description of Material | Ancestors Starved for Two Generations | Ancestors Starved for Three Generations |
|--|---------------------------------------|---|
| Ancestors starved for one generation: | | |
| USDC series: | USDDC series: | |
| Mean..... | - .0043 ± .0168 | |
| Standard deviation..... | - .0141 ± .0119 | |
| Coefficient of variation..... | - .2442 ± .2193 | |
| FSDC series: | FSDDC series: | |
| Mean..... | + .0091 ± .0174 | |
| Standard deviation..... | + .0291 ± .0123 | |
| Coefficient of variation..... | + .4599 ± .2059 | |
| NHDC series: | NHDDC series: | |
| Mean..... | + .0278 ± .0172 | |
| Standard deviation..... | - .1095 ± .0121 | |
| Coefficient of variation..... | - 2.0101 ± .2198 | |
| Ancestors starved for two generations: | | |
| NDDC series: | | NDDDC series: |
| Mean..... | | + .1636 ± .0194 |
| Standard deviation..... | | - .0012 ± .0137 |
| Coefficient of variation..... | | - .4291 ± .2571 |

starvation than for two. Compare the results for number of pods per plant, and for seeds per pod.

The inter-ramal differences appear in Tables XIII-XVI. Of the 28 comparisons, direct and cross, of mean number of ovules, 18 are negative and 10 positive; that is, in 18 cases, the plants with starved ancestry have a lower number of ovules per pod. Thus the deviation

TABLE XIII

| Description of Material | Ancestors Starved for One Generation NHDC | Ancestors Starved for Two Generations NHDDC |
|---|--|--|
| Ancestors well fed for one generation: | | |
| NDHC series: | | |
| Mean..... | + .1495 ± .0172 | + .1773 ± .0147 |
| Standard deviation..... | + .1450 ± .0121 | + .0355 ± .0103 |
| Coefficient of variation..... | + 2.2359 ± .2227 | + .2258 ± .1892 |
| Ancestors well fed for two generations: | | |
| NHHC series: | | |
| Mean..... | - .0312 ± .0175 | - .0034 ± .0151 |
| Standard deviation..... | + .0614 ± .0124 | - .0481 ± .0106 |
| Coefficient of variation..... | + 1.1682 ± .2243 | - .8419 ± .1913 |
| NDHHC series: | | |
| Mean..... | + .2249 ± .0167 | + .2527 ± .0141 |
| Standard deviation..... | + .1333 ± .0118 | + .0238 ± .0100 |
| Coefficient of variation..... | + 1.8417 ± .2179 | - .1684 ± .1836 |
| Ancestors well fed for three generations: | | |
| NHHHC series: | | |
| Mean..... | + .0442 ± .0174 | + .0720 ± .0149 |
| Standard deviation..... | + .0367 ± .0123 | - .0728 ± .0105 |
| Coefficient of variation..... | + .5391 ± .2238 | - 1.4710 ± .1908 |

from the equality of division, if there were no influence of the environment of ascendants, is 4 ± 1.79 . Of the 28 differences, 16 are thrice their probable errors; 9 are significantly negative and 7 significantly positive.

Taking averages, regarding signs, we have:

| | |
|-------------------------------|-------|
| Navy, Within Strains, $A = +$ | .0150 |
| Ne Plus Ultra, $A = -$ | .0819 |
| White Flageolet, $A = -$ | .0378 |

TABLE XIV

| Description of Material | Ancestors Starved for Two Generations <i>NDDC</i> | Ancestors Starved for Three Generations <i>NDDC</i> |
|---|--|--|
| Ancestors well fed for one generation: <i>NDHC</i> series: | | |
| Mean..... | $-.1099 \pm .0180$ | $+.0537 \pm .0164$ |
| Standard deviation..... | $+.0393 \pm .0127$ | $+.0381 \pm .0116$ |
| Coefficient of variation..... | $+.9934 \pm .2394$ | $+.5643 \pm .2140$ |
| Ancestors well fed for two generations: <i>NHHC</i> series: | | |
| Mean..... | $-.2906 \pm .0183$ | $-.1270 \pm .0167$ |
| Standard deviation..... | $-.0443 \pm .0129$ | $-.0455 \pm .0118$ |
| Coefficient of variation..... | $-.0743 \pm .2410$ | $-.5034 \pm .2159$ |
| <i>NDHHC</i> series: | | |
| Mean..... | $-.0345 \pm .0175$ | $+.1291 \pm .0159$ |
| Standard deviation..... | $+.0276 \pm .0124$ | $+.0264 \pm .0113$ |
| Coefficient of variation..... | $+.5992 \pm .2349$ | $+.1701 \pm .2090$ |
| Ancestors well fed for three generations: <i>NHHHC</i> series: | | |
| Mean..... | $-.2152 \pm .0182$ | $-.0516 \pm .0166$ |
| Standard deviation..... | $-.0690 \pm .0129$ | $-.0702 \pm .0118$ |
| Coefficient of variation..... | $-.7034 \pm .2404$ | $-1.1325 \pm .2154$ |

TABLE XV

| Description of Material | Ancestors Starved for One Generation <i>USDC</i> | Ancestors Starved for Two Generations <i>USDC</i> |
|---|---|--|
| Ancestors well fed for one generation: <i>USSC</i> series: | | |
| Mean..... | $-.1705 \pm .0160$ | $-.1748 \pm .0163$ |
| Standard deviation..... | $+.0385 \pm .0113$ | $+.0244 \pm .0115$ |
| Coefficient of variation..... | $+1.0739 \pm .2047$ | $+.8297 \pm .2088$ |
| <i>USHC</i> series: | | |
| Mean..... | $-.0261 \pm .0171$ | $-.0304 \pm .0174$ |
| Standard deviation..... | $+.0029 \pm .0121$ | $-.0112 \pm .0123$ |
| Coefficient of variation..... | $+.1141 \pm .2223$ | $-.1301 \pm .2263$ |
| Ancestors well fed for two generations: <i>USHHC</i> series: | | |
| Mean..... | $-.0426 \pm .0166$ | $-.0469 \pm .0168$ |
| Standard deviation..... | $-.0245 \pm .0117$ | $-.0386 \pm .0120$ |
| Coefficient of variation..... | $-.3385 \pm .2145$ | $-.5827 \pm .2186$ |

TABLE XVI

| Description of Material | Ancestors Starved for One Generation <i>FSDC</i> | Ancestors Starved for Two Generations <i>FSDDC</i> |
|---|--|--|
| Ancestors well fed for one generation: <i>FSSC</i> series: | | |
| Mean..... | - .1315 \pm .0173 | - .1224 \pm .0151 |
| Standard deviation..... | + .0037 \pm .0122 | + .0328 \pm .0107 |
| Coefficient of variation..... | + .3366 \pm .2037 | + .7965 \pm .1769 |
| <i>FSHC</i> series: | | |
| Mean..... | - .0236 \pm .0183 | - .0145 \pm .0162 |
| Standard deviation..... | - .0420 \pm .0130 | - .0129 \pm .0115 |
| Coefficient of variation..... | - .6393 \pm .2166 | - .1794 \pm .1916 |
| Ancestors well fed for two generations: <i>FSHHC</i> series: | | |
| Mean..... | + .0280 \pm .0169 | + .0371 \pm .0145 |
| Standard deviation..... | - .0320 \pm .0119 | - .0029 \pm .0102 |
| Coefficient of variation..... | - .5904 \pm .1997 | - .1305 \pm .1723 |

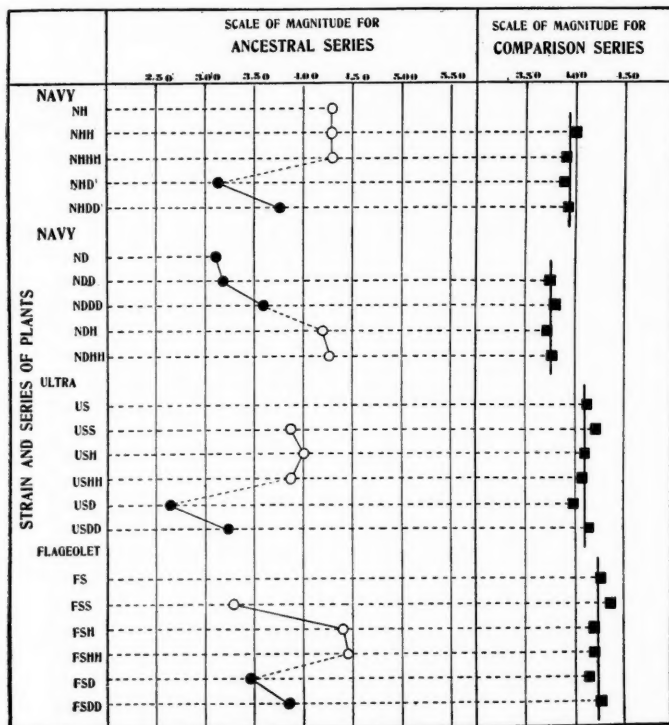


DIAGRAM 10. Mean number of seeds per pod. Compare explanation of diagram 6.

The results for Navy are slightly positive, for the other two varieties more conspicuously negative. The mean of the four varieties is $-.0291$.

Regarding only the 10 direct inter-ramal comparisons, we note that 7 are negative and 3 positive; 3 significantly negative and none significantly positive. The mean of the negative differences is $-.0771$, of the positive $+.0794$, of all $-.0316$.

The data are available for any one caring to work out the relationships for variabilities. The discussion of this point is reserved until further series are gotten.

C. Number of Seeds per Pod

Tables XVII-XIX give the essential biometric constants for number of seeds per pod. Diagram 10 justifies the same general conclusions for the mean number of seeds as were drawn from Diagram 9 for mean number of ovules per pod. In one case, however, the average for seeds is lower on a feeding plot than on the starvation fields.³

Appealing again to constants and their probable errors, we have the results set forth in the tables of fundamental differences, XX-XXIV.

The intra-ramal comparisons, Table XX, show three positive and one negative difference. Two of the positive differences are probably and the third possibly statistically significant. Note, however, that the age of the seed may be a disturbing factor. Compare the results for number of pods and number of ovules.

Of the 28 inter-ramal comparisons, Tables XXI-XXIV, 15 are negative and 13 positive.

In the usual manner, we get for the means:

| | |
|-----------------------|--------------|
| Navy, Within Strains, | $A = +.0078$ |
| Ne Plus Ultra, | $A = -.0711$ |
| White Flageolet, | $A = -.0383$ |

³ Why FSS plants did not mature their seeds well I have never been able to make out. The fact was noticed at harvest time.

For Navy the positive difference is trivial; the negative difference for Ne Plus Ultra and for White Flageolet is much larger.

Considering statistical significance to be indicated by a difference thrice its probable error, we find that 8 are significantly negative and 4 significantly positive. These 4, and 2 of the 8 significantly negative differences, fall in the comparisons between the two strains of Navy and hence can not be given much weight. Of the 20 inter-racial comparisons, direct and cross, within the same strain, 11 are negative and 9 are positive in sign. Of the 10 direct comparisons 5 are positive and 5 negative in

TABLE XVII

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>NH</i> | 4.2555 \pm .0193 | 1.4113 \pm .0136 | 33.1634 \pm .3538 |
| <i>NHH</i> | 4.2672 \pm .0073 | 1.2893 \pm .0052 | 30.2134 \pm .1323 |
| <i>NHHH</i> | 4.2777 \pm .0082 | 1.2802 \pm .0058 | 29.9268 \pm .1463 |
| <i>NHD</i> | 3.1269 \pm .0117 | 1.2964 \pm .0083 | 41.4611 \pm .3068 |
| <i>NHDD</i> | 3.7493 \pm .0116 | 1.2672 \pm .0082 | 33.7974 \pm .2420 |
| <i>ND</i> | 3.0971 \pm .0196 | 1.1143 \pm .0139 | 35.9804 \pm .5017 |
| <i>NDD</i> | 3.1872 \pm .0189 | 1.1984 \pm .0134 | 37.6013 \pm .4752 |
| <i>NDDD</i> | 3.5823 \pm .0176 | 1.1709 \pm .0124 | 32.6870 \pm .3823 |
| <i>NDH</i> | 4.1797 \pm .0108 | 1.2363 \pm .0076 | 29.5786 \pm .1982 |
| <i>NDHH</i> | 4.2512 \pm .0112 | 1.1774 \pm .0079 | 27.6963 \pm .2003 |
| <i>NHHC</i> | 4.0115 \pm .0194 | 1.3959 \pm .0137 | 34.7973 \pm .3812 |
| <i>NHHHC</i> | 3.8979 \pm .0181 | 1.3683 \pm .0128 | 35.1028 \pm .3656 |
| <i>NHDC</i> | 3.9417 \pm .0221 | 1.3616 \pm .0156 | 34.5444 \pm .4405 |
| <i>NHDDC</i> | 3.9333 \pm .0191 | 1.3585 \pm .0135 | 34.5397 \pm .3816 |
| <i>NDDC</i> | 3.7550 \pm .0254 | 1.2798 \pm .0179 | 34.0838 \pm .5301 |
| <i>NDDDC</i> | 3.8191 \pm .0227 | 1.3215 \pm .0161 | 34.6033 \pm .4679 |
| <i>NDHC</i> | 3.7333 \pm .0192 | 1.2989 \pm .0136 | 34.7927 \pm .4058 |
| <i>NDHHC</i> | 3.7751 \pm .0173 | 1.2835 \pm .0123 | 34.0005 \pm .3603 |

TABLE XVIII

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>USS</i> | 3.8781 \pm .0114 | 1.3760 \pm .0081 | 35.4817 \pm .2330 |
| <i>USH</i> | 4.0097 \pm .0146 | 1.2599 \pm .0103 | 31.4219 \pm .2810 |
| <i>USHH</i> | 3.8698 \pm .0214 | 1.3253 \pm .0151 | 34.2475 \pm .4347 |
| <i>USD</i> | 2.6322 \pm .0291 | 1.2235 \pm .0206 | 46.4812 \pm .9367 |
| <i>USDD</i> | 3.2268 \pm .0297 | 1.2823 \pm .0210 | 39.7382 \pm .7453 |
| <i>USC</i> | 4.1269 \pm .0175 | 1.3177 \pm .0124 | 31.9296 \pm .3297 |
| <i>USSC</i> | 4.2113 \pm .0204 | 1.3126 \pm .0144 | 31.1673 \pm .3739 |
| <i>USHC</i> | 4.1045 \pm .0226 | 1.3280 \pm .0160 | 32.3553 \pm .4283 |
| <i>USHHC</i> | 4.0832 \pm .0204 | 1.3333 \pm .0145 | 32.6536 \pm .3899 |
| <i>USDC</i> | 3.9718 \pm .0213 | 1.3403 \pm .0150 | 33.7456 \pm .4192 |
| <i>USDDC</i> | 4.1519 \pm .0214 | 1.2752 \pm .0151 | 30.7127 \pm .3969 |

TABLE XIX

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|--------------|-------------------------|---------------------------------------|---|
| <i>FSS</i> | 3.2918 \pm .0113 | 1.4772 \pm .0080 | 44.8741 \pm .2868 |
| <i>FSH</i> | 4.3907 \pm .0131 | 1.3078 \pm .0093 | 29.7865 \pm .2288 |
| <i>FSHH</i> | 4.4563 \pm .0143 | 1.3095 \pm .0101 | 29.3856 \pm .2450 |
| <i>FSD</i> | 3.4624 \pm .0230 | 1.2993 \pm .0163 | 37.5263 \pm .5323 |
| <i>FSDD</i> | 3.8548 \pm .0021 | 1.1991 \pm .0145 | 31.1063 \pm .4109 |
| <i>FSC</i> | 4.2865 \pm .0172 | 1.3677 \pm .0122 | 31.9072 \pm .3113 |
| <i>FSSC</i> | 4.3643 \pm .0198 | 1.4532 \pm .0140 | 33.2987 \pm .3541 |
| <i>FSHC</i> | 4.1941 \pm .0200 | 1.3610 \pm .0141 | 32.4494 \pm .3701 |
| <i>FSHHC</i> | 4.1997 \pm .0167 | 1.3941 \pm .0118 | 33.1948 \pm .3102 |
| <i>FSDC</i> | 4.1574 \pm .0236 | 1.3596 \pm .0167 | 32.7024 \pm .4428 |
| <i>FSDDC</i> | 4.2710 \pm .0178 | 1.3537 \pm .0126 | 31.6950 \pm .3220 |

TABLE XX

| Description of Material | Ancestors Starved for Two Generations | Ancestors Starved for Three Generations |
|--|---|--|
| Ancestors starved for one generation: | | |
| <i>USDC</i> series: | | |
| Mean..... | <i>USDDC</i> series: + .1801 \pm .0302 | |
| Standard deviation..... | - .0651 \pm .0213 | |
| Coefficient of variation..... | - 3.0329 \pm .5773 | |
| <i>FSDC</i> series: | | |
| Mean..... | <i>FSDDC</i> series: + .1136 \pm .0296 | |
| Standard deviation..... | - .0059 \pm .0209 | |
| Coefficient of variation..... | - 1.0074 \pm .5475 | |
| <i>HDC</i> series: | | |
| Mean..... | <i>HDDC</i> series: - .0084 \pm .0292 | |
| Standard deviation..... | - .0031 \pm .0206 | |
| Coefficient of variation..... | - .0047 \pm .5828 | |
| Ancestors starved for two generations: | | |
| <i>DDC</i> series: | | |
| Mean..... | | <i>DDDC</i> series: + .0641 \pm .0341 |
| Standard deviation..... | | + .0417 \pm .0241 |
| Coefficient of variation..... | | + .5195 \pm .7070 |

sign, but none of the positive differences are statistically significant, while 3 of the negative differences are from 4 to 8 times their probable errors. The mean of the 5 negative differences is $-.1371$, of the 5 positive differences $+.0482$, of the whole series $-.0445$.

D. Weight of Seed

Throughout the experiments partially described in this paper, attention has been given to the weight of the individual seed. From the practical standpoint, the total weight of the seeds produced by the plant would have been a more desirable determination, but for several reasons this was not feasible.

For all the ancestral series, the seeds were weighed individually in units of .025 gram, but the excessive labor involved precluded this for the twenty comparison crops. Instead, the seeds of each series were mixed thoroughly among themselves and random drawings

TABLE XXI

| Description of Material | Ancestors Starved for One Generation <i>NHDC</i> | Ancestors Starved for Two Generations <i>NHDDC</i> |
|---|--|--|
| Ancestors well fed for one generation: | | |
| <i>NDHC</i> series: | | |
| Mean..... | + .2084 ± .0293 | + .2000 ± .0270 |
| Standard deviation..... | + .0627 ± .0207 | + .0596 ± .0192 |
| Coefficient of variation..... | - .2483 ± .5989 | - .2530 ± .5570 |
| Ancestors well fed for two generations: | | |
| <i>NHHC</i> series: | | |
| Mean..... | - .0698 ± .0294 | - .0782 ± .0272 |
| Standard deviation..... | - .0343 ± .0208 | - .0374 ± .0192 |
| Coefficient of variation..... | - .2529 ± .5826 | - .2594 ± .5394 |
| <i>NDHHC</i> series: | | |
| Mean..... | + .1666 ± .0281 | + .1582 ± .0258 |
| Standard deviation..... | + .0781 ± .0199 | + .0750 ± .0183 |
| Coefficient of variation..... | + .5439 ± .5691 | + .5392 ± .5248 |
| Ancestors well fed for three generations: | | |
| <i>NHHHC</i> series: | | |
| Mean..... | + .0438 ± .0286 | + .0354 ± .0263 |
| Standard deviation..... | - .0067 ± .0202 | - .0098 ± .0186 |
| Coefficient of variation..... | - .5584 ± .5725 | - .5631 ± .5285 |

TABLE XXII

| Description of Material | Ancestors Starved for Two Generations <i>NDDC</i> | Ancestors Starved for Three Generations <i>NDDDC</i> |
|---|---|--|
| Ancestors well fed for one generation: | | |
| <i>NDHC</i> series: | | |
| Mean..... | + .0217 ± .0318 | + .0858 ± .0297 |
| Standard deviation..... | - .0191 ± .0225 | + .0226 ± .0211 |
| Coefficient of variation..... | - .7089 ± .6676 | - .1894 ± .6194 |
| Ancestors well fed for two generations: | | |
| <i>NHHC</i> series: | | |
| Mean..... | - .0256 ± .0320 | - .1924 ± .0299 |
| Standard deviation..... | - .1161 ± .0225 | - .0744 ± .0211 |
| Coefficient of variation..... | - .7135 ± .6529 | - .1940 ± .6035 |
| <i>NDHHC</i> series: | | |
| Mean..... | - .0201 ± .0307 | + .0440 ± .0285 |
| Standard deviation..... | - .0037 ± .0217 | + .0380 ± .0203 |
| Coefficient of variation..... | + .0833 ± .6409 | + .6028 ± .5905 |
| Ancestors well fed for three generations: | | |
| <i>NHHHC</i> series: | | |
| Mean..... | - .1429 ± .0312 | - .0788 ± .0290 |
| Standard deviation..... | - .0885 ± .0220 | - .0468 ± .0206 |
| Coefficient of variation..... | - .0190 ± .6440 | - .4995 ± .5938 |

TABLE XXIII

| Description of Material | Ancestors Starved for One Generation <i>USDC</i> | Ancestors Starved for Two Generations <i>USDDC</i> |
|---|--|--|
| Ancestors well fed for one generation: | | |
| <i>USSC</i> series: | | |
| Mean..... | - .2395 ± .0295 | - .0594 ± .0296 |
| Standard deviation..... | + .0277 ± .0208 | - .0374 ± .0209 |
| Coefficient of variation..... | +2.5783 ± .5617 | - .4546 ± .5453 |
| <i>USHC</i> series: | | |
| Mean..... | - .1327 ± .0310 | + .0474 ± .0311 |
| Standard deviation..... | + .0123 ± .0219 | - .0528 ± .0220 |
| Coefficient of variation..... | +1.3903 ± .5993 | -1.6426 ± .5840 |
| Ancestors well fed for two generations: | | |
| <i>USHHC</i> series: | | |
| Mean..... | - .1114 ± .0295 | + .0687 ± .0296 |
| Standard deviation..... | + .0070 ± .0209 | - .0581 ± .0209 |
| Coefficient of variation..... | +1.0920 ± .5725 | +1.9409 ± .5564 |

TABLE XXIV

| Description of Material | Ancestors Starved for One Generation <i>FSDC</i> | Ancestors Starved for Two Generations <i>FSDDC</i> |
|---|--|--|
| Ancestors well fed for one generation: | | |
| <i>FSSC</i> series: | | |
| Mean..... | - .2069 ± .0308 | - .0933 ± .0266 |
| Standard deviation..... | - .0936 ± .0218 | - .0995 ± .0188 |
| Coefficient of variation..... | - .5963 ± .5670 | -1.6037 ± .4786 |
| <i>FSHC</i> series: | | |
| Mean..... | - .0367 ± .0309 | + .0769 ± .0268 |
| Standard deviation..... | - .0014 ± .0219 | - .0073 ± .0189 |
| Coefficient of variation..... | + .2530 ± .5771 | - .7544 ± .4906 |
| Ancestors well fed for two generations: | | |
| <i>FSHHC</i> series: | | |
| Mean..... | - .0423 ± .0289 | + .0713 ± .0244 |
| Standard deviation..... | - .0345 ± .0204 | - .0404 ± .0173 |
| Coefficient of variation..... | - .4924 ± .5406 | -1.4998 ± .4471 |

made for mass weighings.⁴ It is on these samples of 2,000 or more seeds (weighed after drying for several months)⁵ that the averages are based.

Seed weight will be touched rather lightly in this paper. This is in part due to the fact that the seeds for the comparison series could not be weighed individually, thus

⁴ This was the plan for all but *USC* and *FSC*, where 100 seeds, or as many as were available, were weighed *en masse* for each line. From these, the general population mean was calculated.

⁵ The plants were harvested and dried in an empty greenhouse in the early autumn of 1910; stored in an unheated building for the early part of the winter; counted during a period extending from January to early April; and left in the laboratory till weighing, some time in June.

affording data from which the variabilities and probable errors might be calculated. It is in part due to the fact that (as will be clear later) the starvation conditions available seem not to have affected seed weight as they did the other characters with which we deal.

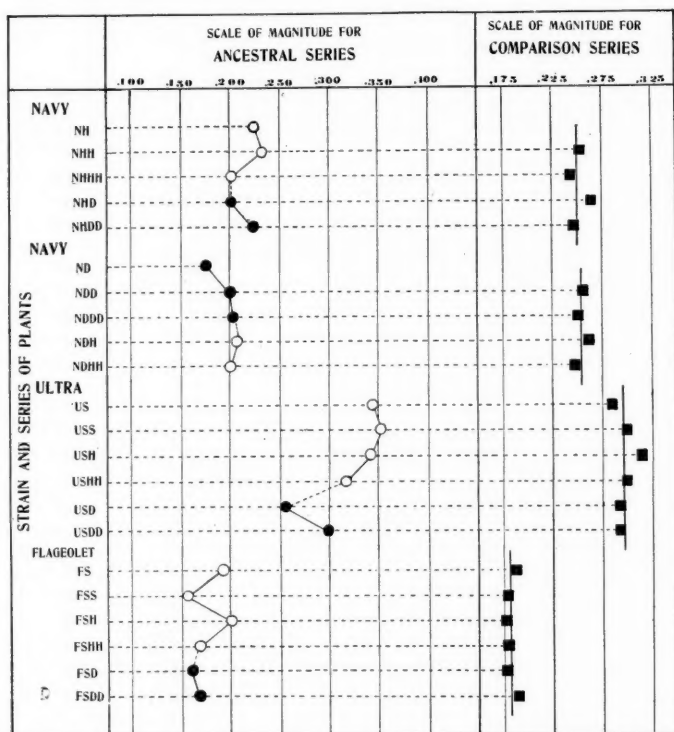


DIAGRAM 11. Mean weight of seeds. Compare diagrams 6, 9 and 10.

The mean weight for both ancestral and comparison series are shown in decimals of grams in Table XXV.

That seed weight is a character influenced by environmental conditions is apparent from the scatter of the means in the ancestral field of Diagram 11 as compared with their closeness to line in the comparison panel. But

the diagram also shows at once that seed weight has not been influenced by the starvation conditions as other characters have. Whereas, with a single exception, number of pods per plant, number of ovules per pod and number of seeds per pod were all conspicuously reduced, seed weight is sometimes higher, sometimes lower, on the starvation plots. Of the 28 differences, 21 are negative in sign, as compared with 28 for pods per plant and ovules per pod and 27 for seeds per pod.

Expressing numerically the same differences for the ancestral series as are usually taken for the comparison series, we find for comparisons within the strains:

TABLE XXV

| Ancestral Series | | | Comparison Series | | |
|------------------|-------|--------|-------------------|-------|--------|
| Series | N | Mean | Series | N | Mean |
| <i>FS</i> | 3,000 | .19322 | <i>FSC</i> | 7,562 | .18587 |
| <i>FSS</i> | 3,740 | .15636 | <i>FSSC</i> | 2,000 | .18026 |
| <i>FSH</i> | 2,122 | .20039 | <i>FSHC</i> | 2,000 | .17893 |
| <i>FSHH</i> | 1,788 | .16813 | <i>FSHHC</i> | 2,000 | .18145 |
| <i>FSD</i> | 1,989 | .16140 | <i>FSDC</i> | 2,000 | .17816 |
| <i>FSDD</i> | 1,643 | .16783 | <i>FSDDC</i> | 2,000 | .19027 |
| <i>US</i> | 2,391 | .34491 | <i>USC</i> | 9,879 | .28450 |
| <i>USS</i> | 3,271 | .35349 | <i>USSC</i> | 2,000 | .29933 |
| <i>USH</i> | 1,165 | .34261 | <i>USHC</i> | 2,000 | .31450 |
| <i>USHH</i> | 530 | .31642 | <i>USHHC</i> | 2,000 | .30147 |
| <i>USD</i> | 1,002 | .25474 | <i>USDC</i> | 2,000 | .29170 |
| <i>USDD</i> | 789 | .29948 | <i>USDDC</i> | 2,000 | .29284 |
| <i>NHH</i> | 7,334 | .23186 | <i>NHHC</i> | 2,000 | .25430 |
| <i>NHHH</i> | 5,601 | .20274 | <i>NHHHC</i> | 2,000 | .24407 |
| <i>NHD</i> | 6,630 | .20073 | <i>NHDC</i> | 2,000 | .26616 |
| <i>NHDD</i> | 5,029 | .22293 | <i>NHDDC</i> | 2,000 | .24669 |
| <i>NDD</i> | 2,362 | .19968 | <i>NDDC</i> | 2,000 | .25849 |
| <i>NDDD</i> | 1,946 | .20374 | <i>NDDDC</i> | 2,000 | .25207 |
| <i>NDH</i> | 3,227 | .20879 | <i>NDHC</i> | 2,000 | .26248 |
| <i>NDHH</i> | 2,433 | .20261 | <i>NDHHC</i> | 2,000 | .24815 |

Navy, $A = -.0047$

Ne Plus Ultra, $A = -.0604$

White Flageolet, $A = -.0103$

General Average, $A = -.0231$

Thus there appears to be a distinct influence of the de-pauperization of the individual upon the weight of the seeds which it produces. But modification of weight is very slight indeed as compared with that of the other characters.

Considering now the weight of the seeds produced by the comparison plants, we note that of the 28 differences which may be taken (within and between strains) between plants of luxuriant and those of depauperate ancestry, 15 are negative and 13 are positive in sign, a deviation of only 1 ± 1.79 from the expected 14:14 ratio.

Of the individual differences, the largest is .023 gram, while most of them fall, towards zero. Averaging we get:

| | |
|-----------------------|--------------|
| Positive Differences, | + .00915 gr. |
| Negative Differences, | — .00831 gr. |
| All Differences, | — .00020 gr. |

Surely values as low as this can not give much weight to the assertion that depauperization of the parents has had any influence upon the weight of the seed of the offspring plants.

Looked at in a preliminary and superficial way (and it hardly seems worth while to go into the matter more minutely until other data are tabled and reduced), the data seem to indicate that the weight of the seed is a character much less directly dependent upon cultural conditions than are the vegetative characters of the plant. Conditions which reduce these latter may not materially affect seed weight.

Possibly, the environmental complexes available were such as to affect certain characteristics of the ancestral plants, while leaving others, *i. e.*, seed weight, unmodified. Possibly, seed weight is a character little affected by external conditions of any kind. These are questions which can only be solved by further experiments designed to determine whether some environmental complexes regularly affect seed weight while others do not, and to ascertain what influence, if any, such reduction has upon the characteristics of offspring seeds.

E. Combination Characters

Some characteristics are combinations of two or more individual measurements. Such are, for example, the

correlation between two dimensions, or the ratio of the one to the other.

The only case of this kind to be considered here is the coefficient of fecundity, which is simply the ratio of the total seeds matured by a population of pods to the total ovules formed. The values are given in Table XXVI.

For the ancestral series all but 2 of the 20 comparisons within strains show lower fecundity in the starved series. Taking averages:

| | |
|-----------------------|--------------|
| Navy, Within Strains, | $A = -.0790$ |
| Ne Plus Ultra, | $A = -.1178$ |
| White Flageolet, | $A = +.0075$ |

Thus Navy and Ne Plus Ultra mature about 7-11 per cent. more of their ovules on feeding than on starvation fields. Apparently, White Flageolet is not affected.

TABLE XXVI

| Ancestral Series | | | Comparison Series | | |
|------------------|--------|-------|-------------------|-------|-------|
| Series | Pods | C.F. | Series | Pods | C.F. |
| <i>FS</i> | — | — | <i>FSC</i> | 2,876 | .7387 |
| <i>FSS</i> | 7,809 | .5789 | <i>FSSC</i> | 2,457 | .7057 |
| <i>FSH</i> | 4,541 | .7899 | <i>FSHC</i> | 2,117 | .6903 |
| <i>FSHH</i> | 3,837 | .8080 | <i>FSHHC</i> | 3,180 | .6971 |
| <i>FSD</i> | 1,449 | .6984 | <i>FSDC</i> | 1,506 | .6869 |
| <i>FSDD</i> | 1,556 | .7680 | <i>FSDDC</i> | 2,646 | .7046 |
| <i>US</i> | — | — | <i>USC</i> | 2,569 | .7032 |
| <i>USS</i> | 6,605 | .7015 | <i>USSC</i> | 1,888 | .7389 |
| <i>USH</i> | 3,406 | .7787 | <i>USHC</i> | 1,570 | .7389 |
| <i>USHH</i> | 1,743 | .7386 | <i>USHHC</i> | 1,936 | .7329 |
| <i>USD</i> | 802 | .5518 | <i>USDC</i> | 1,810 | .7184 |
| <i>USDD</i> | 851 | .6724 | <i>USDDC</i> | 1,619 | .7516 |
| <i>NHH</i> | 14,029 | .7884 | <i>NHHC</i> | 2,355 | .7087 |
| <i>NHHH</i> | 11,230 | .7965 | <i>NHHHC</i> | 2,614 | .6979 |
| <i>NHD</i> | 5,581 | .6625 | <i>NHDC</i> | 1,733 | .7002 |
| <i>NHDD</i> | 5,449 | .7501 | <i>NHDDC</i> | 2,308 | .6953 |
| <i>NDD</i> | 1,827 | .7326 | <i>NDDC</i> | 1,159 | .6992 |
| <i>NDDD</i> | 2,018 | .7596 | <i>NDDDC</i> | 1,542 | .6901 |
| <i>NDH</i> | 5,955 | .8136 | <i>NDHC</i> | 2,077 | .6813 |
| <i>NDHH</i> | 5,019 | .8224 | <i>NDHHC</i> | 2,494 | .6985 |

For the comparison series grown from these seeds, we find that of the 20 comparisons, direct and cross, within the strains, 12 show lower and 8 show higher fecundity in the offspring of starved plants. The means are:

| | |
|------------------|---------------|
| Navy, | $A = -.00036$ |
| Ne Plus Ultra, | $A = -.00615$ |
| White Flageolet, | $A = -.00196$ |

Discussion of such differences is obviously superfluous.

IV. RECAPITULATION, DISCUSSION AND TENTATIVE CONCLUSIONS

The purpose of the series of investigations, described in part, is to ascertain whether the depauperization of the individual through the environmental complexes constituting "poor" agricultural conditions, influences the characteristics of its offspring, and if so, how much. The problem of the chemical and physical "causes" of the depauperization has received the most intensive experimental consideration. The question of the influence of the surroundings of the ascendants upon the characteristics of the descendants has been much more a matter of speculation. Yet the second of these problems is of obvious importance to the agriculturist and of interest to the evolutionist concerned with environmental factors. The time seems ripe, therefore, for its consideration on the basis of extensive quantitative experimental data.

Notwithstanding the great progress which has been made in the investigation of the relationship of the chemical and physical properties of the substratum to the characteristics of the plant, the diversity of results and the clash of theories show that we have only entered the edge of this field of research. In consideration of these facts, and especially in view of the all but unsurmountable difficulties of controlling in large experiments the conditions of growth of flowering plants, it has seemed necessary in first studies to choose merely good and bad growing conditions as indicated by yields in actual cultures. Thus the methods are avowedly and intentionally of the rough and ready sort. If in such experiments an unquestionable influence of the conditions

of growth of the ascendants upon the characteristics of the descendants be demonstrated, it will be worth while to determine the weight to be given to individual physical and chemical factors in the ascendant environment. If, on the other hand, there be no detectable effect of ancestral depauperization, then the cost of elaborate batteries of experiments had better be devoted to some other problem.

This first study is based upon three varieties of one species, *Phaseolus vulgaris*. The conclusions should not, therefore, be extended to other forms with different demands upon the soil, habits of growth or type of seed. This is true not merely on general principles, but is especially important because of the well-known capacity of this species for growth under adverse conditions.

The characters considered are number of pods per plant, number of ovules formed and number of seeds matured per pod, ratio of total seeds ripened to total ovules laid down—the coefficient of fecundity—and weight of seeds.

Constants are based upon the countings of number of ovules and seeds in about 130,000 pods and weighings of over 110,000 carefully selected seeds. But these observations were drawn from only 21,000 individual plants. As the results in the body of the paper show, these numbers are too small rather than unnecessarily large for a problem of this delicacy. I believe, however, that they are sufficiently large to bring the probable errors of random sampling low enough that dangers of erroneous conclusions lie rather in the inevitable experimental (and to a less extent observational) errors.

Bearing in mind the difficulties to be surmounted and the consequent possibilities of error, we draw the following tentative conclusions.

Environmental conditions which greatly reduce number of pods per plant, number of ovules formed per pod and number of seeds matured per pod, affect to a less degree the relative number of seeds matured, *i. e.*, the

coefficient of fecundity, and have but little effect upon seed weight.

The influence of the modification of the ascendants upon the characteristics of the descendants is extremely slight. There seems, nevertheless, to be a definite reduction in the number of pods per plant and number of ovules per pod. There is also a possible lowering of the absolute and relative number of seeds per pod. Apparently, there is no modification of seed weight.

COLD SPRING HARBOR, N. Y.

STRUCTURAL RELATIONS IN XENOPARASITISM

W. A. CANNON

DESERT BOTANICAL LABORATORY

At various times normally independent plants have been experimentally caused to grow and develop within the tissues of other independent plants, deriving from this arrangement food and food-materials and organizing tissues and organs.¹ Although in themselves short-lived, the artificial parasites offer interesting suggestions as to the possible conditions under which true parasitism may arise in nature.² It is clear, for instance, that the mutual relation of parasite and host is extremely complex, both from a purely physiological point of view and from a structural one. On the one hand, it presupposes suitable osmotic relations and not unfavorable chemical reactions, and on the other, among other things, the fitting and exact adjustment of the tissues of the parasite, and it signifies atrophies as well.

When we observe the leading structural changes which normally occur in the growth of a haustorium of a habitual parasite, such, for example, as the mistletoe,³ we find a course of development which is full of suggestions. A young haustorium is composed mainly of undifferentiated ground tissue, but there are the beginnings of conductive tissue within, and a protective epidermis without. Upon the commencement of the parasitic relation the most marked changes occur. In the first place epithelial cells

¹ "Artificial Parasitism, etc.," G. J. Peirce, *Bot. Gaz.*, **33**: 214, 1904.
² "The Condition of Parasitism in Plants," D. T. MacDougal and W. A. Cannon, Publ. No. 129 Carnegie Inst. of Wash., 1910. "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

³ "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

⁴ "The Anatomy of *Phoradendron villosum*," W. A. Cannon, *Bull. Torr. Bot. Club*, 1901.

are formed directly from parenchyma, and then after penetrating the host, such of the periphery of the haustorium as touches non-living cortical host cells, organizes cork. Finally, upon the attainment by the haustorium of the woody cylinder the conductive tissue of the haustorium opposes cell for cell the conductive tissue of the host, and in such parasites as possess sieve-tubes, the sieve-tubes hold a similar relation to the sieve-tubes of the host.⁴ It happens therefore in habitual parasites that a portion of the development of the haustoria occurs after the parasitic relation has been entered into, so that the direction of the development of much of the tissue of the haustorium is fortuitous, depending in part on the position occupied by the tissues of the host.

DURATION OF THE XENOPARASITIC RELATION

Although induced parasitism means naturally a limited period during which the artificial relation can be continued, this period varies greatly with the different nutritive couples. A review of this phase of the subject will not be given here, as it is completely presented in the papers referred to above, but two or three of the most pertinent parasitic relations will be cited. Peirce grew *Pisum sativum* on *Vicia Faba* to maturity (Peirce, "Artificial Parasitism," *l. c.*). MacDougal (see above) records many experiments of which the following may be given: *Cissus laciniata* was grown on *Opuntia blakeana* from February 1, 1908, until April 19, 1909, and another culture, which is especially treated in this paper, lasted from early autumn, 1911, to June 10, 1912. In the instances where *Cissus* was employed roots were freely formed, the stem attained considerable length and organized tendrils and leaves. From these facts a large capacity for adjustment on the part of the induced parasites is exhibited, and also a degree of physiological adaptability is shown which reveals something of the plasticity of such plants and argues a fair suitability for the dependent relation.

⁴"On the Structure of the Haustoria of Some Phaneorgamic Parasites," G. J. Peirce, *Ann. Bot.*, 7: 324, 1893.

XENOPARASITISM OF *CISSUS LACINIATA*

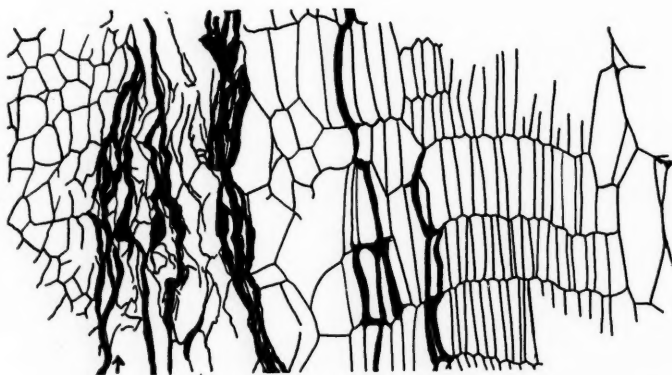
The induced parasite *Cissus laciniata* exhibits in the structure and form of its roots (the shoot was not studied) certain deviations from the normal which are of significance and interest. A history of the experiments in which this species was used as a parasite is given in another place, suffice it to state here that a cutting of the Mexican grape (*Cissus laciniata*) was introduced into the tissues of *Opuntia blakeana* and allowed to remain several months. A shoot with leaves and tendrils was formed. After the culture had been running some time a root of the grape was seen to emerge from the surface of the cactus, to grow downwards, and to penetrate the soil. It was severed so that the *Cissus* had connections with the cactus only. On June 10, 1912, the newly organized leaves were seen to be relatively small and the tendrils not to develop. The culture was thereupon taken down and the roots of the parasite dissected out so that their relations to the host tissue might be learned.

All of the roots of *Cissus* which were situated within the tissues of the cactus were found to be fleshy. A main root was traced from the base of the cutting through the tissues of the cactus for a distance of 3 cm. when, as above mentioned, it issued from the cactus and found its way into the soil. This root gave off one branch about 1 cm. from its point of origin, which extended for a distance of 3 cm. into the tissues of the cactus. The root last mentioned gave rise in turn to a branch which attained a length of 1.5 cm. In addition to these roots there were several short ones which reached little beyond the surface of the parent root. All roots except the one especially mentioned as not behaving in this manner were wholly enclosed within tissues of the host.

STRUCTURE OF FREE-LIVING ROOTS

The portion of the roots which are free-living offer useful points of comparison, for which purpose the anatomy will be briefly reviewed.

A root 2.0 mm. in diameter shows the usual divisions into central cylinder and cortex. The endodermis is well marked. The epidermis is discolored and bears the remains of root-hairs. Cork has not begun to form, however. The cortex is composed of cubical parenchyma; the parenchyma of the central cylinder offers no unusual features. Little starch or crystals are to be seen.



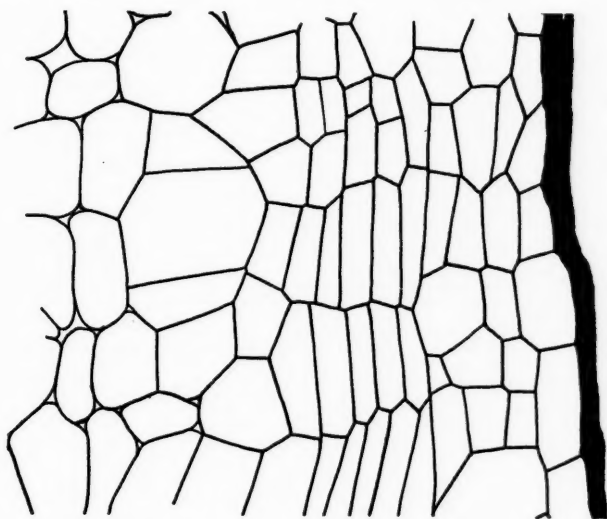
ANATOMICAL RELATION OF THE *Cissus-Opuntia* COUPLE. On the left appears the extra-cortical portion of the root with the limit indicated by the arrow. On the right is the wound tissue of the cactus, and between this and the root lies disorganized cactus cells.

STRUCTURE OF THE PARASITIC ROOTS

The roots of *Cissus*, which developed within the tissues of the cactus, varied in diameter from 2 to 5 mm. and showed characteristics which were in certain regards quite different from those of the free-living roots examined.

If a cross-section of a root 2 mm. in diameter is studied the usual differentiation into cortex and central cylinder will be noted. The cortex is composed of relatively large cells a few of which contain stellate crystal aggregates and raphides. A layer of cork, over half dozen cells in thickness, bounded by the dead remains of the epidermis,

lies on its periphery. The remains of root-hairs were looked for but were not found. A well defined endodermis with granular contents, a portion of which is starch, limits the cortex on its inner surface. The central cylinder has relatively wide medullary rays and a large pith containing much starch. Opposite each



CROSS-SECTION OF PARASITIC ROOT OF *Cissus laciniata* SHOWING THE FORMATION OF CORK AND THE DISORGANIZED EPIDERMIS.

bundle, and about 2 cells inside the endodermis, there is a plate which may be composed of leptome, and which in some favorable material appears to be thickened wall only.

A root 5 mm. in diameter has essentially the same structure as the smaller one above described. The main differences lie in the heavier cork and the thicker cortex. The plate which lies opposite each fibro-vascular bundle, also, is heavier. The endodermis is noticeably poorer in starch.

TISSUES OF THE HOST

The structure of the flat stems of *Opuntia*, broadly speaking, consists of thin-walled, large parenchyma, through which there course strands of conductive tissue. Protection of the stem is afforded by a heavy cuticularized epidermis.

When the parasitic relation is entered into, wound tissue, with heavy outer walls in certain cells similar to those of the cork, is formed about the injury caused by the introduction of the cutting. The cutting sends out adventitious roots which penetrate the parenchymatous tissue of the host, and sooner or later these roots are surrounded by wound tissue which the host promptly organizes as a result of the unusual stimulation. By this formation the water-storing ground tissue of the host is separated from the living cells of the parasite.

TISSUE RELATIONS OF PARASITE AND HOST

In rapidly growing roots, contact is made with the living parenchyma of the cactus, and the parasite is in physical position to absorb foods and food materials. In instances, however, where root growth is slow, wound tissue is formed by the cactus, and the parasitic relation is not favorable for absorption. Following the formation of wound tissue cork is organized by the parasite, so that the cushion of non-living material separating host and parasite in the older portions of the culture, comes to be derived from both species.

When one compares the structural relations of a haustorium of a habitual parasite with the analogous absorbing organ of such a xenoparasite as *Cissus*, several suggestive inferences may be derived. The relation may be presented briefly in the following parallel:

| <i>Xenoparasite</i> | <i>Parasite</i> |
|-----------------------------|-----------------------|
| No special digestive cells. | Epithelium developed. |
| Root-hairs suppressed. | No root-hairs formed. |

Foods and food materials enter haustorial root through epidermis.

Cork formed after establishment, following organization of wound tissue by host.

Tissues articulate with the corresponding host tissues.

Meristematic tissue localized.

Foods and food materials enter haustorium through parenchyma, sieve-tubes, and vessels.

Terminal portions at least of all permanent tissues formed after establishment.

The same.

Meristematic tissue not localized.

The parallel given above suggests, as intimated in another paragraph, that any species which is to become dependent on another species possesses to a large degree the power of adaptability and morphological plasticity, so that the direction of the development of its tissues or organs can to a degree be modified. Atrophies result, and the assumption of unaccustomed functions, and tissues are organized in harmony with tissue formation, or other physiological activity on the part of the host.

SHORTER ARTICLES AND DISCUSSION

ON TRICOLOR COAT IN DOGS AND GUINEA-PIGS

AFTER reading Dr. Castle's short article on this subject I want to make a few remarks. His explanation of the peculiar inheritance of the lemon and white and tricolor colors in Galton's Bassett hounds will have to be somewhat modified. For it is impossible to compare tricolor dogs and tricolor guinea-pigs. Tricolor dogs are never irregularly spotted with black and yellow, as tricolor guinea-pigs, cats or rabbits, but they are in reality either black and tan, or else sable, spotted with white. My attention being drawn to the subject of tricolor dogs by Galton's paper, I have never neglected an opportunity to observe dogs of this color, in dog-shows and from illustrations. Some tricolor breeds, as the fox terrier, are black and tan, spotted with white, others, as nearly all the hounds, are sable, still others, such as collies, may be either black and tan or sable, spotted with white. I have never seen an exception, such as a dog with a yellow spot on the back and a black foot.

For the rest, I think Dr. Castle's explanation is quite correct; it all depends upon the place of the spots upon a sable dog, whether these will be yellow or black. A spot on a dog of sable color, *e. g.*, a fox hound, will always be black if it is on the animal's back. If on the muzzle, or on a foot, or far down on the side, it will always be yellow, a spot, *e. g.*, on the shoulder may be partially black, partially yellow, shading off from one color into the other.

It is of course possible that some of the Bassett hounds in the pack recorded by Galton were real yellow and whites, and we know from the evidence of breeders of dachshunds that yellow can be dominant over black and tan or sable in dogs. So it may be possible that in that pack two real lemon-and-whites (*e. g.*, such as had a yellow spot on the back) have sometimes given tricolor young, but in those cases in which two tricolor parents gave lemon and white offspring, I feel sure, such young were of that color only because they happened not to be pigmented in a spot where sable dogs show black color.

It would certainly be interesting to try and find illustrations of Galton's hounds, especially of the lemon and white ones of tricolor parentage.

In rabbits, there exist three wholly different classes of tricolor animals. In the first place there are the real tricolors, those animals which, if they were not partially albinistic, would be irregularly spotted with black, agouti, blue or chocolate on a yellow ground. They are comparable to the tricolor black-yellow-white, blue-cream-white, etc., guinea-pigs and to the tricolor cats. Secondly, there are those animals which are black and tans, or blue (or chocolate) and tans, spotted with white. These are comparable to the tricolor fox terriers, tricolor goats and the so-called tricolor mice, which are sable, spotted with white.¹

Thirdly, there are those rabbits which, if not partially albinistic, would be "tortoise-shell," and which are comparable to the spotted "tortoise" mice.

I think Galton's hounds may have all been alike except for the distribution of the pigmented patches on the coat. Those hounds with the less white would then be called black and tan, or sable; those with much white would be called tricolor, or lemon and white, or even black and white, according as to where the colored patches fell.

I am not so sure Galton's black and tan hounds must necessarily have been partially albinistic, as in dogs the partially albinistic ones are generally so because of the presence of a factor (or factors) absent from wholly colored ones. (In other words, spotting with white is dominant in some dogs.)

The distribution of the colored area over partially albinistic animals assuredly depends upon the cooperation of so many factors (amongst which there are very probably some non-genetic ones) that on our hypothesis the production of tricolor young from yellow and white parents, and *vice versa*, becomes very well possible.

AREND. L. HAGEDOORN

VERRIÈRES LE BUISSON

¹"The Genetic Factors in the Development of the Housemouse," A. L. Hagedoorn, *Zeitschr. f. indukt. Abst. und Vererbungslehre*, 1911, Bd. VI, Heft 3.

NOTES AND LITERATURE

THE CLASSIFICATION OF THE LIVERWORTS

BOTANISTS have long felt that the classification of the liverworts was very much in need of revision, and any serious attempt to establish a classification that will better express the real inter-relationship of the Hepaticæ is very welcome. The valuable series of papers recently published by Dr. Cavers,¹ on the classification of the Bryophytes, is a distinct contribution to the subject, and is a decided advance over any classification that has been proposed hitherto.

Dr. Cavers is well known to students of the liverworts through a series of papers of exceptional merit, published at intervals during the past few years. The present publication presents at length the conclusions he has reached as a result of his studies on these important plants.

It is still too early to expect a definitive classification of the liverworts, as there are still a good many important types whose development is incompletely known, and it is also highly probable that there are still forms awaiting discovery which we may reasonably expect will throw light upon some relationships which are still obscure.

Dr. Cavers has made a careful study of the work of the most recent investigators, as well as of the older standard works, and while one may take exception to a few of his deductions, still, as a whole, one will agree with his main conclusions, and will welcome this contribution of his as a decided advance in our knowledge of the inter-relationships of the Bryophytes. The Bryophytes (or "mosses," using this term in its widest sense) are forms of peculiar interest to students of plant-morphology, especially to those engaged in the problems of the origin of the higher types of plants; since the Bryophytes occupy an intermediate place between the aquatic algæ and the ferns which are typically land plants. While there is decided difference of opinion as to how the ferns originated, the weight of evidence

¹"The Inter-relationships of the Bryophyta," by Frank Cavers, D.Sc., F.L.S. (*New Phytologist*, Reprint No. 4), Cambridge; at the Botany School, 1911.

is strongly on the side of their direct derivation from some liverwort-like ancestor. It is this question that makes a thorough study of the liverworts of such great importance in seeking for an explanation of the origin of the vascular plants.

Aside from this, however, the Bryophytes, especially the liverworts or Hepaticæ, are exceptionally interesting, as they show in a remarkably clear way many adaptations to special environmental influences.

The Bryophytes are divided, usually, into two main groups—the Liverworts (Hepaticæ), and the True Mosses (Musci). One peculiar order, Anthocerotales, the “Horned Liverworts,” is sometimes considered to represent a third class, coordinate with the Musci and Hepaticæ. Cavers does not accept this view, but considers them to represent an order only of the Hepaticæ.

Aside from the Anthocerotales, the liverworts usually are divided thus into two orders, Marchantiales and Jungermanniales. There are, however, several genera that to a certain extent combine characters of both of these orders and sometimes have been assigned to one, sometimes to the other. Of these genera *Spharocarpus* may be cited. This is, on the whole, probably the simplest known liverwort, and is represented in the United States by several species in the warmer parts of the country. Much like *Spharocarpus* is a peculiar liverwort, *Geothallus*, known as yet only from San Diego in Southern California. A third genus, *Riella*, evidently related to these, is an aquatic type, only recently found in America. All of these are very simple liverworts and probably stand near the base of the liverwort series. They may, perhaps, be regarded as synthetic types connected with both of the main series of liverworts. Cavers proposes to unite them into a special order, Sphærocarpales, and this conclusion will probably be accepted as representing best their position in the system. In the Sphærocarpales, as interpreted by Cavers, the sporophyte or neutral generation is of simple structure, and the elaters which in the typical liverworts accompany the spores are represented by undifferentiated sterile cells.

From some form probably not very unlike *Spharocarpus*, but with perhaps a still simpler sporophyte, it is probable that the two lines of development, the Marchantiales and the Jungermanniales have diverged. Within these two orders the course of development can be easily traced, as nearly all the stages in the

evolution of the two groups are represented by existing genera. It is hard to say which of the two orders should be considered the more primitive, as the lower members of each are of about equal complexity, and can be derived equally well from some form allied to *Sphærocarpus*.

Sphærocarpus has been associated most commonly with the Ricciaceæ, the lowest of the Marchantiales, but there are certain genera of the Jungermanniales that in many ways show a close resemblance to the Sphærocarpaceæ, and make it almost certain that there is a real relationship existing between them. These similarities are found both in the character of the thallus and reproductive organs, as well as in the early history of the embryo. They may be only cases of parallel development, but it is quite as likely that they are true homologies. Two genera, *Petalophyllum* and *Fossombronia*, which have always been placed in the Jungermanniales, are especially suggestive of a possible connection with the Sphærocarpales, and it is by no means impossible that it may turn out that these genera, and possibly some others, should be removed from their association with the Jungermanniales and transferred to the Sphærocarpales.

THE MARCHANTIALES

The Marchantiales constitute a very natural order, whose simplest members, the Ricciaceæ, are sometimes separated as a distinct order. There does not seem to be any valid reason for this, however, as the Ricciaceæ are connected with the more highly specialized Marchantiaceæ by a number of intermediate forms.

The Marchantiales are comparatively few in number, probably not more than three hundred species being known; but their relatively large size and characteristic appearance make them the most conspicuous of the liverworts, the common and widespread *Marchantia polymorpha* being the most familiar liverwort to most students of botany. The dichotomously branched thallus, with its elaborate systems of tissues, probably may be said to represent the highest type of a strictly thallose plant.

Within the Marchantiales are many interesting cases of adaptation, and a very complete series of forms exists showing the evolution of the elaborate and highly specialized thallus of *Marchantia* and similar genera, from the much simpler type

found in *Riccia*. The elaboration of the sporophyte can also be followed. *Riccia*, as is well known, has the simplest known sporophyte, in this respect being in a much lower plane than *Spharocarpus*, although the thallus in the latter is much less specialized than in *Riccia*.

The evolution of the sporophyte, as every botanist knows, is associated with a reduction in the amount of tissue devoted to spore-production, and a corresponding increase in the purely vegetative or sterile tissue of the sporophyte. The latter, however, in the Marchantiales always remains relatively simple in structure.

In the lower Marchantiales the sexual organs are borne upon the dorsal surface of the unmodified thallus, but in the more highly specialized types like *Fimbriaria* or *Marchantia*, characteristic receptacles are developed, usually composed of a number of very short branches resulting from the repeated dichotomy of the original thallus apex. The classification of the Marchantiales has been based largely on the character of the receptacle and the sporogonium.

Cavers recognizes five families of very unequal size, viz., Ricciaceæ, Corsiniaceæ, Targioniaceæ, Monocleaceæ and Marchantiaceæ. The latter, which aside from the Ricciaceæ, comprises the greater part of the Marchantiales, was divided by Leitgeb into three subfamilies, Astroporæ, Operculatæ and Compositæ, but it is very doubtful whether these can be maintained.

The Ricciaceæ, the great majority of which belong to the genus *Riccia*, are undoubtedly the simplest, and probably the most primitive, members of the order. The extremely simple sporophyte is almost entirely devoted to spore production, there being no sterile tissue beyond a very imperfect single outer layer of cells. No other liverworts approach the Ricciaceæ in the simplicity of the sporophyte.

The second family, Corsiniaceæ, is intermediate in the structure of the sporophyte, between the Ricciaceæ and the higher Marchantiales.

The third order, Targioniaceæ, includes the two small genera, *Targionia* and *Cyathodium*. These are very characteristic liverworts represented in the United States by a single species *Targionia hypophylla*, common in the coast region of California, but absent from the eastern states. This species occurs also in southern and western Europe. *Cyathodium* includes a few

species of delicate liverworts inhabiting dark crevices in rocks, or shallow caves. All the species show evidences of marked structural modifications due to their unusual habitat. *C. fetidissimum* is a characteristic species of the Indo-Malayan region.

The simple genus *Monoclea* with two species represents very distinct the family Monocleaceae. In his great work on the Hepaticae, Leitgeb referred *Monoclea* to the Jungermanniales, and this view was adopted by Schiffner in his treatment of the Hepaticae in Engler & Prantl's "Natürliche Pflanzenfamilien." This association with the Jungermanniales was mainly on account of the structure of the thallus, which is quite destitute of the air-chambers which distinguish most of the Marchantiales. There is also in *Monoclea* no definite archegonial receptacle, and the solitary sporogonium has a long seta like that of many Jungermanniales.

All the more recent students of *Monoclea*, however, are agreed that the plant really belongs to the Marchantiales, this being shown both by the structure of the thallus, and that of the reproductive organs. The absence of air-chambers is with little question to be looked upon as a secondary condition, due to the semi-aquatic habit of the plant. A similar disappearance of the air-chambers is known in the unmistakable marchantiaceous genus *Dumortiera*.

Leitgeb, in his important memoirs on the Hepaticae, recognized three types of archegonial receptacle. Only in one of these was the receptacle compound in its structure. More recent studies, including those of Cavers, indicate that this compound or "composite" type is much more general than Leitgeb supposed. Cavers states that probably all of the genera of the Marchantiaceae, except *Clevea* and *Plagiochasma*, will be found to have receptacles of the composite type.

In tracing the phylogeny of the Marchantiales, Cavers distinguishes two main divergent groups which are connected with the Ricciaceae by *Corsinia* and *Boschia*, respectively. The first series includes, among other genera, *Clevea*, *Plagiochasma*, *Reboulia* and *Fimbriaria*, the latter representing the culmination of this series.

The second series, starting with *Boschia*, shows two main branches, one including the Targioniaceae and *Monoclea*, the other the most highly developed genera, like *Fegatella*, *Dumor-*

tieria and *Marchantia*. The latter genus is the most highly specialized of all the Marchantiales.

THE JUNGERMANNIALES

Much the greater number of liverworts belong to the Jungermanniales. The classification of this large order is very much in need of revision, as it is at present in a very unsatisfactory condition.

They are generally divided into two series of very unequal size, this division being based upon the position of the archegonium—and are denominated the Anaerogynæ and Aerogynæ. In the former the growing point of the shoot persists indefinitely, while in the latter, in the fertile shoots, it is sooner or later transformed into an archegonium, and the sporogonium is therefore terminal.

The name Metzgeriaceæ was later proposed by Underwood, as a substitute for Leitgeb's Anaerogynæ, the Aerogynæ being alone called Jungermanniaceæ. Cavers thinks these two divisions are largely artificial, and it must be admitted that there is much to be said for his view.

Comparing the Jungermanniales, as a whole, with the Marchantiales, it is seen that in the former specialization has been in the direction of external differentiation, *i. e.*, in most of them a more or less definite axis, bearing leaves, is present, but the tissues remain quite uniform. In the Marchantiales, on the other hand, the plant is a thallus, but the tissues are of various kinds.

The simplest of the Jungermanniales, *e. g.*, *Aneura*, *Pellia*, etc., have a very simple thallus, either composed of quite similar cells, or with a midrib which may possess a strand of special conductive tissue. The simplest type of thallus is quite like that of *Spharocarpus*, and may very well have originated from some similar type.

In these thallose Jungermanniales there is frequently a tendency toward the development of marginal lobes, which may bear a quite definite relation to the primary divisions of the single apical cell of the thallus. Such marginal lobes are undoubtedly homologues of the leaves found in the more highly specialized leafy liverworts—the "Aerogynæ," of Leitgeb. Sometimes these leaf-like organs of the anaerogynous liverworts are very distinct, as in *Treubia*, and the transition to the typical leafy liverworts

like *Porella* or *Frullania*, is a very gradual one. It is very clear that this tendency towards leaf-development has arisen in a number of quite disconnected genera, and this of course suggests a multiple origin for the Acrogynæ.

Cavers proposes four families of the lower, or anacrogynous, Jungermanniales, viz., Aneuraceæ, Blyttiaceæ, Codoniaceæ, Calobryaceæ. He thinks that the first three are more or less artificial, and it is very certain that it will be necessary when some of the less known genera are more fully investigated, to make a radical revision of these families. The Calobryaceæ, on the other hand, forms a sharply defined and natural family, comprising two genera, *Haplomitrium* and *Calobryum*. Cavers concludes that there are two main lines of development within the Anacrogynæ, one including the Codoniaceæ and Calobryaceæ, the other the Blyttiaceæ and Aneuraceæ, suggesting that the two latter families might perhaps be better united into a single one. There seems to be little question that the two families are closely related through such forms as *Umbraculum* and *Podomitrium*.

There is much uncertainty as to the limits of certain genera. This is especially the case with the genus *Calycularia*, to which have been assigned species which further investigation has shown to belong to quite different families. The writer has had occasion recently to examine carefully the structure of *Calycularia radiculosa*, a rare species from Java. Schiffner concluded that this species should be removed from the genus *Calycularia*, of the family Codoniaceæ, and united with *Mörkia*, a member of the Blyttiaceæ. While it is certainly distinct from the true species of *Calycularia*, it is equally certain that it can not be assigned to *Mörkia*. It will probably have to be separated into a distinct genus with characters intermediate between those of the Codoniaceæ and the Blyttiaceæ. In short, it is very clear that at present a satisfactory classification of the group is not feasible.

The Aneuraceæ and Blyttiaceæ show an interesting type of specialization of the thallus which is wanting in the Codoniaceæ and Calobryaceæ, where the tendency is toward the development of leaf-like lobes foreshadowing the leaves of the leafy liverworts. In *Podomitrium* and *Umbraculum*, assigned respectively to the Blyttiaceæ and Aneuraceæ, the thallus is differentiated into a prostrate cylindrical rhizome and erect dichotomously branched fan-shaped shoots, which resemble very closely the deli-

cate leaves of certain filmy ferns, for which these liverworts might easily be mistaken.

In the development of the sporophyte the *Anacrogynæ* show a decided advance over the *Marchantiales*. There may be developed a considerable amount of sterile tissue in the capsule; aside from the ordinary elaters, and this sterile tissue sometimes assumes the form of a sort of columella or "elaterophore," suggesting the columella found in the *Anthocerotaceæ*, and possibly homologous with it. This elaterophore may be either apical (*Aneura*) or basal (*Pellia*).

While recognizing the entirely independent origin of leaves in several lines of the *Anacrogynæ*, nevertheless Cavers is inclined to believe that all of the true leafy liverworts (*Acrogynæ*) can be traced back to a single type which he thinks is best represented by *Fossombronia*, which genus he places at the top of the series *Codoniaceæ*. It may be said, however, that there are some strong arguments in favor of a polyphyletic origin for the *Acrogynæ*—a view which has been defended by several students of the group.

There are, as we have already stated, good reasons for believing that *Fossombronia* should not be associated with *Pellia* and the other *Codoniaceæ*, but associated with the *Sphaerocarpaceæ*, as the highest member of a series of which *Sphaerocarpus* and *Geothalus* are lower members. This interpretation would not interfere with the acceptance of Cavers's view that some at least of the leafy liverworts have been derived from forms like *Fossombronia*.

The acrogynous *Jungermanniales*, or leafy liverworts, include much the larger part of existing liverworts. Of about 250 genera and 4,500 species of known liverworts, all but 60 genera and 700 species belong to the acrogynous *Jungermanniales*. They are nevertheless comparatively uniform in type, and Cavers believes that they may all be traced back to a common ancestral type allied to *Fossombronia*.

With very few exceptions they show a single tetrahedral apical cell and usually three series of leaves corresponding to the three lateral faces of the apical cell. The ventral leaves (amphigastria) are not infrequently absent, and both dorsal and ventral leaves often show various modifications, among the most striking of which are hollow sacs presumably developed for water storage.

The tissues are very simple, and only very rarely is there any specialization of cells for conduction or other purposes. In size

they range from almost microscopic forms like some of the minute epiphyllous *Lejeuniaceæ*, to stout species like some of the tropical *Frullanias*, which form pendant masses several feet in length.

In all the *Aerogynæ* the archegonia are in groups terminating the fertile branch, whose further growth is arrested by the transformation of the apical cell into an archegonium.

The sporogonium is always well developed, usually showing a well-marked foot and seta. Perfect elaters are always present. A small number only of the *Aerogynæ* have been studied critically with reference to the development of the sporophyte, and much more work must be done before the real affinities of some of the genera can be determined satisfactorily.

On the basis of our present knowledge of the group, Cavers proposes a classification based largely upon the work of Spruce. He recognizes two main divisions, the first including a single very large family, *Lejeuniaceæ*, with nearly 2,000 species; the second contains seven families, of which three, viz., *Porellaceæ*, *Pleuroziaceæ* and *Radulaceæ*, are regarded as natural families, the other four as more or less artificial, the limits between them being difficult to define.

The inter-relationships of the *Aerogynæ* are extremely difficult to follow. A number of students of the liverworts, notably Spruce and Schiffner, believe that the group is of polyphyletic origin, the *Lejeuniaceæ* representing a quite distinct line derived from forms allied to the *Aneuraceæ*. There are striking resemblances both of gametophyte and sporophyte, the former in some cases having a protonemal stage of long duration, and very much resembling one of the simpler thallose liverworts. Cavers believes, however, that these resemblances are simply parallel developments, and not true homologies; and, as already stated, that the *Aerogynæ* represent a single line of development. Of these forms he states that *Lophozia* probably comes nearer to the assumed ancestral type.

From the *Lophozia* type, three branches are traced, one through *Plagiochila* developing a large number of genera, among which *Cephalozia*, again, is the starting-point for the development of a number of specialized genera like *Zoopsis*, *Lepidozia*, and *Trichocolea*. The second line leads through *Marsupiella* and *Nardia* to a number of genera, of which the highest are *Stephaniella*, *Gyrothyra* and *Symphyomitra*. The third line,

beginning with *Lophozia*, leads through *Sphenolobus* to the great family Lejeuniaceæ, and to the characteristic genera *Porella* and *Frullania*, which may be considered to represent the most perfectly developed characters of the whole order.

THE ANTHOCEROTALES

The Anthocerotales, Cavers's fifth order of Hepaticæ, comprise a comparatively small number of liverworts of very peculiar structure, and very readily distinguished from all other plants. The differences between them and the other liverworts are so marked that they are sometimes considered a class—Anthocerotes—coordinate, on the one hand, with all the other liverworts, on the other with the true mosses.

The structures of the four genera which are comprised in the order are so much alike that they can all be assigned without question to a single family, Anthocerotaceæ.

The gametophyte is of simple structure, and all the cells much alike, each as a rule containing a single large chromatophore resembling that of many green algæ. The reproductive organs, both archegonia and antheridia, show certain peculiarities, which in some ways have their nearest approximation among the lower ferns, and in connection with the characters of the sporophyte suggest a real connection between the ferns and the Anthocerotalea.

The sporophyte differs much from that of the other liverworts. In all of the Anthocerotaceæ, except possibly some species of *Notothylas*, the spore-producing tissue all arises from the outer region (amphithecium) formed by the first periclinal divisions in the capsule, and much the greater part of the tissue of the sporophyte remains sterile. In all cases a large foot is present, and above it a zone of actively dividing cells is present, which may retain its activity for several months, so that the sporophyte may attain a length of 10 centimeters or more. As the outer tissues are in most cases well provided with chlorophyll, and sometimes with stomata, a complete photosynthetic apparatus is established much in advance of anything found in the other Hepaticæ.

This long-continued growth of the sporophyte is associated with a central strand of conducting tissue (columella), which is reminiscent of the axial vascular bundle of the young sporo-

phyte of some of the lower ferns to which the sporophyte of *Anthoceros* shows the closest resemblance known in the Bryophyta.

Within the Anthocerotaceæ is an interesting series connecting the small sporophyte of *Notothylas* with its relatively large development of sporogenous tissue, and the large sporophyte of *Anthoceros* with a small amount of sporogenous tissue and a highly developed photosynthetic system.

It is, at present, impossible to say whether or not the type of *Notothylas* is a reduced one. Cavers believes it is a primitive type from which the more highly developed genera, culminating in *Anthoceros*, have been derived. He is inclined to minimize the importance of certain striking features, *e. g.*, the peculiar chloroplasts and the endogenous antheridia, and thinks the differences between the Anthocerotales and the other liverworts are not sufficient to warrant their separation into distinct classes. He considers the columella of the Anthocerotaceæ may be connected with the true liverworts through the Sphærocarpales, which they resemble in a number of particulars.

It may be noted, in passing, that there is a possibility of a connection of the Anthocerotaceæ with some of the lower Marchantiales. The Targioniaceæ, especially *Cyathodium*, for example, show some interesting analogies in the sporogonium with *Notothylas*, and the gametophytes also agree in the presence of large lacunæ, and the chromatophores of *Cyathodium* are also of unusual size.

Cavers's conclusions may be summarized as follows: From some common ancestral form, "Sphæro-Riccia," two lines of development diverged, one leading to the Marchantiales, the other to the Sphærocarpales, which in turn gave rise to the lower Jungermanniales. From some member of the latter, perhaps *Fossombronia*, all of the leafy liverworts arose. Somewhere near the Sphærocarpales it is assumed that the Anthocerotales branched off.

We are inclined to believe that some modifications of this arrangement are likely to be made. It is quite possible that *Fossombronia* should be removed from the Jungermanniales, and associated with the Sphærocarpales; and if Cavers's assumption is correct, that the leafy liverworts (Acrogynæ) have arisen from a prototype resembling *Fossombronia*, this would entirely divorce the two great divisions of the Jungermanniales.

It is doubtful whether the derivation of the Anthocerotaceæ from the Sphærocarpales will be generally accepted. For the present, at least, the order must be regarded as a very isolated one, and perhaps best considered to represent a distinct class.

DOUGLAS HOUGHTON CAMPBELL

STANFORD UNIVERSITY

INVERTEBRATES

UNDER the able leadership of Professors Zeigler and Woltereck there is appearing from Klinkhardt's press in Leipzig a series of excellent small monographs of familiar animals designed for the student, teacher, investigator and amateur who desires to secure a brief but authentic account of the results of systematic, histological, morphological, anatomical and embryological investigations on representative types of animals. Two volumes have already appeared, the frog by Dr. Hempelmann, and the rabbit by Dr. Gerhardt, and the series of invertebrates has been introduced by two volumes, volume 3 of the series on "*Hydra und die Hydroiden*" by Dr. Steche, of Leipzig, and volume 4 by Professor Meisenheimer, of Jena, on "*Die Weinbergschnecke*."

Dr. Steche's volume is designed not merely as a monograph on *Hydra* along the lines on which the series is planned, but adds to these the features of an introduction to the experimental treatment of biological problems as offered by the lower animals. *Hydra* is an exceptionally favorable subject for this treatment by virtue of its hardiness, ease of obtaining and of maintenance, and simplicity of structure. Few invertebrates have served as a basis of so many and so varied experimental tests and have been the object of so many investigations as *Hydra*. With this wealth of results before him it is not to be wondered at that this modest volume is open to the charge of some sins of omission. The choice of topics treated is, however, most catholic and this author has wisely avoided controversial difficulties. The histological and embryological sections are less

¹"Monographien einheimischer Tiere," Herausgegeben von Professor Dr. H. E. Ziegler, Stuttgart, und Professor Dr. R. Woltereck, Leipzig, Bd. 3; "*Hydra und die Hydroiden*. Zugleich eine Einführung in die experimentelle Behandlung biologischer Probleme an niederen Tieren," von Dr. Otto Steche, vi + 162 pp., 65 figs. in text and 2 pls., M. 4, geb. M. 4.80; Bd. 4, "*Die Weinbergschnecke, Helix pomatia*," von Professor Johannes Meisenheimer, 140 pp., 1 pl. and 72 figs. in text, M. 4, geb. M. 4.80.

developed than seems desirable, but in compensation the sections on biology and experimental subjects such as regeneration, regulation, grafting, graft hybrids, effects of external factors on growth and regeneration, polarity and heteromorphosis are well, though concisely, developed. Several pages of practical suggestions as to collection, rearing, feeding and preparing *Hydra* will be found very useful as will also the key to the species. The author conservatively clings to the widely current names *viridis*, *grisea* and *fusca* and rejects the older names of Pallas which strictly have priority.

Half of the book is given to the hydroids. Noteworthy in this are several superb figures of hydroid colonies from the Helgoland Nordsee Museum. A brief list of titles closes the volume from which we note the omission of Nutting's and Mayer's monographs.

The volume by Professor Meisenheimer upon the garden snail follows closely the program of the series, with perhaps less of emphasis upon the experimental and physiological aspects and more space taken for the presentation of the static phases which are greatly increased necessarily over those of a simple animal such as *Hydra*. But there appears still to be call for more expansion on the dynamic aspects of the subject in the case of this volume. The chapter upon the relation of the snail to the environment and to man is a concession in the right direction, and the prevalence of the biological standpoint throughout the anatomical chapters in some measure supplies the physiological data pertinent to the structural phases. These are very clearly and methodically set forth with abundant illustrations, many of which are new. A chapter on other land pulmonate mollusks affords an all too brief basis for comparison of the snail with other mollusks.

Both of these volumes will be exceedingly useful to zoologists in all countries, for the objects with which they deal are cosmopolitan. A similar series of monographic booklets on laboratory types based on American material would be of great value for American students and investigators.

CHARLES ATWOOD KOFOLD

